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RESPONSE OF UNDERSTORY VEGETATION OF SOME BOREAL MIXEDWOOD FOREST COMMUNITIES TO NATIVE UNGULATE FORAGING

by

© MANFRED BICHLMAIER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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Date.....2 April 1985.....

Abstract

In this study the response of some plant community types within the Boreal Mixedwood section of central Alberta was examined in relation to high and low intensity grazingsystems involving native ungulates. The cover, density and frequency of vascular plant species in aspen forest, balsam poplar forest and willow-dominated shrub fens was determined with random quadrats and compared among lightly and heavily grazed stands. The response of the productivity of major shrub species in the forest communities to high grazing levels was examined.

The visual plant cover estimates in each sample quadrat were ordinated using a detrended correspondence analysis. The ordination diagrams showed that the samples were arranged along two major gradients. The three plant community types were spread out along the first axis representing a complex environmental gradient ranging from moderately drained upland soils to organic soils in the lowland. The second axis of the ordination diagram separated samples from lightly and heavily grazed areas. A grazing gradient seems to be a major source of variation in the abundance of plant species.

Statistical differences in the abundance of many plant species in relation to the grazing system were found. The species were classified into decreasers and increasers according to their response pattern. Some preferred forage shrubs (e.g. *Viburnum edule, Prunus virginianus, Amelanchier alnifolia*) and some large herbaceous perennials (e.g.*Aralia nudicaulis, Epilobium angustifolium, Disporum trachycarpum*) were less abundant in the heavily grazed quarter section. Species which had increased in abundance included mainly bristly or spiny shrubs (e.g. *Rubus idaeus, Rosa acicularis, Ribes oxycanthoides*) and some introduced weedy species (*Taraxacum officinale, Galeopsis tetrahit*).

The response of the dominant shrub in the aspen forest, *Corylus cornuta*, to different levels of winter browsing was studied with a simulated browsing experiment. The variation in the production of leaf biomass and of current annual growth of 150 stems of this species could best be explained by differences in stem size and browsing intensity. A response surface fitted

to the productivity data by a polynomial multiple regression analysis showed that production increased steadily with size. The productivity increased at intermediate simulated browsing intensities, but it decreased at higher levels.

The production of leaf biomass, current annual growth and total aboveground biomass of stems of *C. cornuta* and *Amelanchier alnifolia* were compared between the two grazing systems. The frequency distributions of size and biomass showed that browsing ungulates set upper limits to the growth of these shrub species. Significant differences were found among the slopes of logarithmic regression lines of leaf biomass and current annual growth on basal diameter of *C. cornuta* in lightly and heavily grazed stands. Regressions of shrub biomass on shrub size were also computed for *A. alnifolia*, *Cornus stolonifera* and *Salix planifolia*.

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1. Introduction

Herbivores are animals that eat living plant tissues (Crawley 1983). The type of plant tissue ingested varies among the herbivore species as well as with the season and habitat (e.g. Nietfield 1983). Each habitat type has a characteristic association of plant species. Differences in the growth form and the phenology of the plant species affect the quantity and quality of forage available to herbivores through the seasons.

Herbivores may be classified on a scale from generalists to specialists depending on the variety of plant species they feed upon (Belovsky 1981). Large ungulates tend to fall toward the generalist's end of the scale. Nevertheless, they exhibit some forage selectivity which can be demonstrated by plant species which are proportionally more frequent in the diet than in the environment (Petrides 1975). Thus it can be expected that the plant species in a habitat type may be affected to different degrees by foraging ungulates.

In many models of plant-herbivore systems, all plants are aggregated in a single measure of vegetation biomass (Caughley 1976). Forage selectivity and differences in the response of plants to herbivory are disregarded in such models. In structurally and floristically complex plant communities, changes in the abundance of many plant species may alter the forage quality while forage biomass levels remain constant. An investigation of the effects of herbivore abundance on the species composition and the abundance of plant species present in a habitat type must complement the measurement of forage production.

The removal of plant tissues by herbivores rarely results in the death of a perennial plant (Crawley 1983). The plant may compensate for the loss or it may even be stimulated to higher productivity. Utilization by herbivores is only one of many factors influencing plant productivity. A detailed analysis of a large sample of the structural and functional units of a plant species is necessary to separate the effects of herbivore utilization from other major factors causing variability in plant growth.

The Ministik Wildlife Research Station (MWRS) presented an opportunity to study the effects of two grazing systems with dramatically different grazing histories. The first objective

in this study was to quantify the changes in the abundance of plant species within selected habitat types in relation to the grazing intensity. As scarce or poor quality winter forage can be a significant limiting factor for populations of native ungulates, the investigation of the effects of browsing on the productivity of dominant shrub species in the study area was chosen to be the second objective. An experiment was to be designed to test the hypothesis that the level of use would influence the amount of forage produced by shrubs. The productivity of selected shrub species was compared between low and high intensity grazing systems to reveal their effects on shrub growth.

2. Study area

2.1 Location

The MWRS, operated by the Department of Animal Science at the University of Alberta, is located 35 km ESE of the city of Edmonton on the Cooking Lake Moraine (Figure 2.2). This field station comprises 250 ha enclosed by a heavy gauge 2.2 m high game fence. A 65 ha subdivision of this area has been heavily stocked with native ungulates since the station was first established in 1977. The MWRS is surrounded by the Ministik Bird Sanctuary which is managed by Ducks Unlimited Canada. Most of the 7,200 ha of the sanctuary are located in Tp.50, Rg.21, W4 (Russell 1984).

2.2 Land use history

Little is known about the early native people who lived in the area of the Cooking Lake Moraine. Artifacts seem to indicate the presence of Indian hunters in the Beaver Hills since the continental ice sheet disappeared. The first white men in the area were trappers and fur traders of the Hudson's Bay Company coming up the North Saskatchewan River. They reported severe forest fires in the Beaver Hills in 1796 and in 1813/14 (Watson and Polster 1979). In 1870, this region became part of the Dominion of Canada. By 1876, many nomadic Indian bands were confined to reserves defined by Treaty No.6 (Ray 1974). No Indian reserve was established in the Beaver Hills.

As a consequence of the incorporation into the Dominion, the Canadian Prairie Provinces were surveyed. G.A. Simpson and M. Deane conducted the first land survey in the Beaver Hills in 1883 (Nyland 1969). In 1891 the first white settlers arrived. A year later, in response to fires caused by the settlers clearing land, the Cooking Lake Timber Reserve was established. It comprised approximately six townships on the Beaver Hills with "dense forest" used for commercial lumber production (Nyland 1969). While more settlers arrived, some Edmonton residents recognized the recreational potential of the Beaver Hills, particularly that

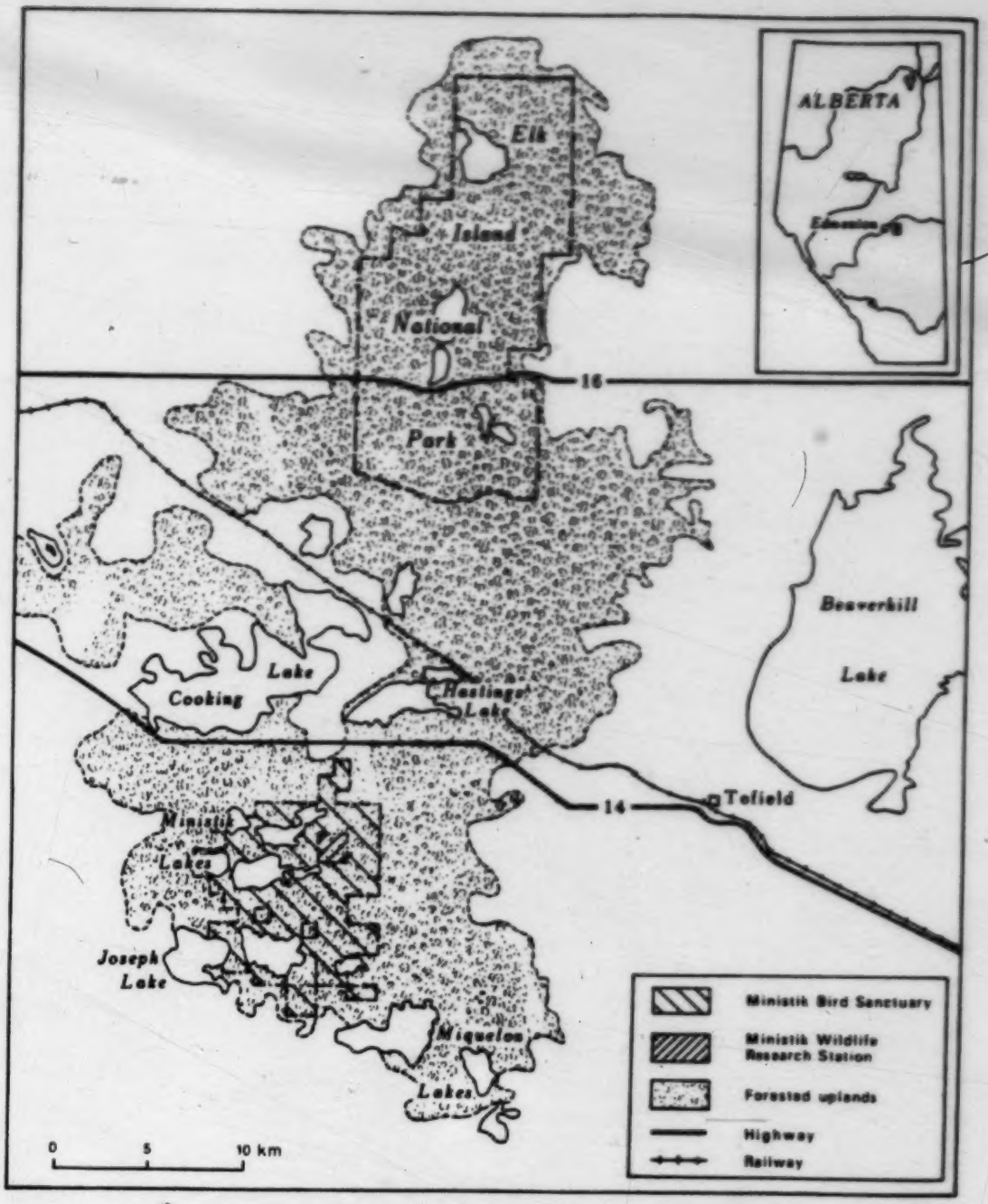

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Figure 2.1: Location of the study area within the Cooking Lake Moraine.

of the Cooking Lake area.

Forest fires remained a common feature. The greatest fire in this region raged all spring and summer of 1895. Nearly all forests on the Cooking Lake Moraine including the ones in the timber reserve were destroyed. Less severe fires were common in the following years. In 1899 the Cooking Lake Forest Reserve, replacing the timber reserve, was established in an attempt to manage reforestation of the area. The 440 km² of this reserve included the area of the present Ministik Bird Sanctuary (Stefiszyn 1983). In 1906 a part of the forest reserve around Astotin Lake was fenced to preserve a herd of naturally occurring elk (*Cervus elaphus canadensis*). The area became Dominion Park in 1913 and National Park in 1930, known as Elk Island National Park (Crown 1977). The size of the park was increased in 1922 and 1947 by incorporation of the northern portion of the forest reserve.

More settlers arrived in the Beaver Hills as plans became known that a railway was going to be built through there. In 1909, the line connecting Winnipeg with Edmonton was completed by the Grand Trunk Pacific Company (Morrow 1964). The same year the forest reserve was reduced to about 287 km² as the area was opened for homesteading (Stefiszyn 1983). In 1910, the first tree nursery in Alberta was started near Cooking Lake. Two years later it was moved to the new forestry headquarters near the south fence of the present Elk Island National Park. Reforestation attempts in the Beaver Hills were not very successful, mainly because a conflict of interests. In a continuous effort to promote the growth of coniferous trees on the Cooking Lake Moraine, F.Kelley, the forest ranger on the reserve, seeded or planted a total area of about 400 ha between the years 1919 to 1930. In those years farmers had recognized the grazing potential of the forest reserve. In 1922, the Blackfoot Stock Association was founded. The Cooking Lake Forest Reserve was fenced and stocked with cattle and horses (Stefiszyn 1983). In 1924 and 1929 fires on the reserve destroyed most of the tree plantations. The status of the forest reserve was cancelled in 1941 (Watson and Polster 1979).

The bird sanctuary around the Ministik Lakes was created by the Dominion government in 1920. It was transferred to the Provincial government in 1930. Before Ducks Unlimited

Canada started to manage the sanctuary in 1938, settlers and their livestock had some effects on the area.

> "Among these were extensive grazing, cutting of hay and illegal shooting, and it is said that there was also poaching of fur-bearing animals and negligence in respect to setting of fires" (Soper 1939).

One section of land in the centre of the sanctuary belonged to the Hudson's Bay Company. The north half of that section was bought in the early or mid 1920's by Mr. G. Horricks, who used it for cattle grazing until 1973 (pers. comm. Isabel Simons). The southern half was bought by Ducks Unlimited Canada (Soper 1939). This section of land is presently occupied by the MWRS. The bird sanctuary has been further increased to include parts of Joseph Lake, Oliver Lake and Larry Lake.

2.3 MWRS layout

After its establishment in 1977, only the northwest quarter of the MWRS was surrounded by a 2.2 m high game fence (Figure 2.2). This enclosure was stocked with elk, moose (*Alces alces*) and bison (*Bison bison*) at varying densities (Table 2.1). Corrals, paddocks and facilities for supplementary feeding were constructed to test the feasibility of a high intensity game farming operation. By 1982, the rest of the section was contained by a game fence. Some animals were released into the three quarter section to investigate the potential of game ranching without supplementary feeding.

2.4 Climate

The regional climate of the study area can be described as dry continental with short warm summers and long cold winters. Unfortunately, representative climatological data are sparse. The nearest recording Atmospheric Environment Service (AES) weather station at Ellerslie (30 km W of MWRS) is at an elevation that is 60 m to 80 m lower than the MWRS. The total annual precipitation recorded at the sanctuary in the 1960's was not significantly different from Ellerslie. The long-term average at Ellerslie is 452 mm/year (period of record:

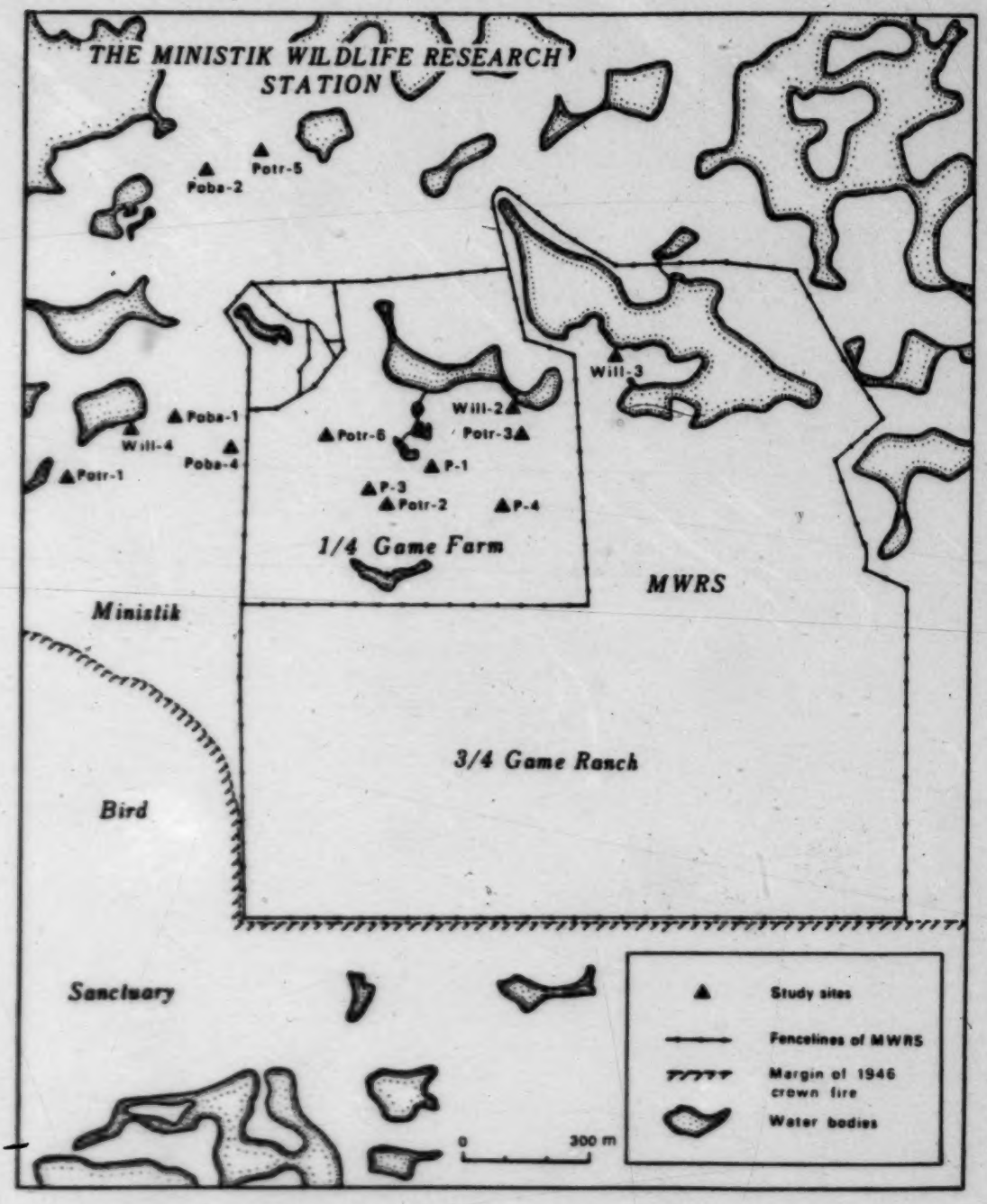

Figure 2.2: Layout of the Ministik Wildlife Research Station (MWRS) and location of study sites (Potr: aspen forest; Poba and P: balsam poplar forest; Will: willow shrub fens).

Table 2.1: Winter stocking rates in the NW quarter section of the MWRS (64 ha) from 1977/78 to 1982/83.

TIME	semi-domesticated *Cervus elaphus*	*Alces alces*	*Bison bison*	wild *Odocoileus* spp.
1977/78	9	2(+)	0	unknown
1978/79	12	3(+)	3	2(+)
1979/80	9	2(+)	5	unknown
1980/81	17	4	5	5(+)
1981/82	21 @	2	7	unknown
1982/83	24	7	12	unknown

Data are from Nietfield (1983) and Annual Reports of Wildlife Production and Management Programme. Department of Animal Science. University of Alberta.

1964-1980). The mean annual temperature at Ellerslie was 2°C and the average frost-free period was 110 days (AES 1981).

2.5 Geology

The Cooking Lake Moraine is underlain by the Edmonton Formation which consists of Upper Cretaceous non-marine shales and sandstone, interbedded with clay ironstone concretionary layers and coal seams (Lang 1974). A preglacial bedrock high accounts for the high elevation (Carlson 1967). The surficial geology is dominated by thick glacial tills deposited by the stagnating Laurentian ice sheet (Jennings 1983). Glaciolacustrine sediments of superglacial lakes are common and they can occur at any topographical location (Crown 1977).

The study area has been mapped as a hummocky dead-ice moraine (Bayrock 1962). Knobs, kettles and prairie mounds are the most characteristic landforms. The high relief is responsible for a pattern of diverse plant communities and soil types as well as for the limited arability of this area.

2.6 Soils

The Cooking Lake Moraine has been mapped as an island of grey wooded soils within the zone of black soils (Odynsky 1962). The transition of these soil types and the prairie-forest ecotone correspond to each other. According to the present classification system, the prairie is characterized by Chernozemic soils. The diagnostic Ah horizon is formed by rapid humification of abundant dead organic material. The major soil forming process in the forest region is the downward leaching of organic and inorganic soil compounds .The result of this process is a Bt horizion which is indicative of Luvisolic soils developed under a persistent forest cover. Most mineral soils in the study area have a well developed Bt horizon which puts them in the Luvisolic Order of the Canadian System of Soil Classification (Canada Soil Survey Committee 1976). An acidic, leached Ae horizon indicates soil development under forest vegetation (Pettapiece 1969). The dominant soils of Elk Island National Park and of the MWRS are

Orthic Gray Luvisols (Crown 1977). Poorly drained mineral soils have mostly been classified as Humic Luvic Gleysols. Organic soils prevail in the numerous depressions. Typic and Terric Mesisols have been found in shrub and sedge fens. Less common are the Fibrisols which have been described from peat bogs. Only one such area occurs in the MWRS.

2.7 Hydrology

Numerous fens, sloughs and lakes fill the depressions of the hummocky topography. Kettles and other low-lying areas are subject to discharge of local or intermediate groundwater flow systems (Meyboom 1967). Crown (1977) regarded the luvisolic character of poorly drained mineral soils as a clear indication for the groundwater recharge nature of the Cooking Lake Moraine.

A clear pattern of surface drainage expressed by a network of stream channels cannot be found in the Beaver Hills. The Beaverhill watershed can be subdivided into several units. These smaller subbasins are generally centered around the larger lakes in the Beaver Hills (Alberta Environment 1976). At high water levels some lakes may be connected with small, inconspicuous creeks (Laycock 1973).

The importance of surface runoff and precipitation for the condition of lakes and wetlands is demonstrated by a long history of water level fluctuations of the major lakes in this region. High lake levels in the 1870's, 1880's and the early part of the 20th century until 1930, as well as smaller rises of water levels in the 1950's and 1974 have been linked to periods of a wetter climate (Alberta Environment 1976). A drop of the water level by 2-3 m since the beginning of this century has been recorded for many lakes in the watershed (EPEC 1971). The climate of the spring and summer of 1983 was wetter than normal.

2.8 Vegetation

The Aspen Parkland is a transitional belt of variable width developed between the major vegetational zones of the Prairie and the Boreal and Cordilleran Forest in Alberta. Moss (1932) first documented that a significant part of this area was dominated by poplar forests rather than by aspen groves interspersed with open grassland. This section of the aspen parkland, with few conifers, he termed "poplar area". Moss further indicated that white spruce (*Picea glauca*) appeared to be the climax tree in a considerable part of this region. The study area lies within the poplar area close to the typical parkland. A survey of the southernmost limit of four species of coniferous trees in the Canadian Prairie Provinces delineated a "transitional forest" whose boundaries are very similar to Moss' poplar area (Zoltai 1975). The transitional forest was defined as the area between the southernmost occurrence of a single coniferous tree, most commonly white spruce, and the line of the southernmost occurrence of all four species (i.e. white spruce, black spruce (*Picea mariana*), tamarack (*Larix laricina*) and pine (*Pinus contorta* or *P.banksiana*).

However, Rowe (1972) classified the Beaver Hills as an isolated outlier of the Boreal Mixedwood section of the Boreal Forest. This designation was mainly based on the dominant tree species. The survey of the ecoregions of Alberta (Strong and Leggatt 1981) took soil characteristics and climatic regimes into account in addition to major vegetation parameters. Again, the Cooking Lake Moraine was mapped as an island within the Aspen Parkland and classified as a dry subregion of the Boreal Mixedwood.

The knob and kettle topography in a large portion of the study area creates a mosaic of plant communities from moderately drained upland sites to poorly or imperfectly drained lowlands. Upland grasslands are rare in the study area. They are restricted to land which has been cleared for pasture at various times. White spruce stands are found occasionally on present or former islands, where they escaped the forest fires, and near present lakeshores. Numerous individual white spruce, scattered over the entire study area, can be found on both upland and lowland sites. The majority of the upland is covered by forests dominated by aspen

(*Populus tremuloides*). In forests with poorly drained mineral soils balsam poplar (*P. balsamifera*) is commonly the most abundant tree. Moss (1932) classified the two forest types as the aspen and balsam poplar consociations, subunits of the poplar association. He recognized that in many forest stands with both poplar species codominating these consociations can be intermixed. A dense understory of shrubs and herbs characterizes each consociation.

The wetland communities in the study area are similar to some described by Jeglum (1972) in the Boreal Mixedwood Section of central Saskatchewan. Emergent fens frame the areas of open water around sloughs or lakes. These communities which have also been called reed-swamps, may be dominated by *Scirpus validus, Typhus latifolia, Sparganium spp., Eleocharis palustris, Carex atherodes* and *Scolochloa festucacea* (Lewis *et al.* 1928). Sedge fens usually surround the emergents and fill many of the numerous depressions. These sometimes extensive meadows are characterized by *Carex rostrata* and *Carex atherodes* (Watson and Polster 1979). The transition from the sedge meadows to the balsam poplar lowland forest is frequently marked by a narrow band of willows (*Salix* spp.). However, such tall shrub fens may completely cover larger low-lying areas (Bishoff 1981). Some smaller sites, on drier organic soils, may be dominated by paper birch (*Betula papyrifera*). Black spruce bogs are found to the north and to the west of the study area, but they have not been encountered in the bird sanctuary. Low shrub fens as described by Jeglum (1972) were not seen in the study area.

3. Plant community survey

3.1 Introduction

The layout of the MWRS provided the opportunity to study two different grazing systems within similar natural surroundings. The NW quarter had been used for the grazing of cattle for almost 50 years before an intensive game farming operation was started in 1977. For several years the quarter section has been heavily stocked with elk and bison (*Bison bison*). Some moose (*Alces alces*) and wild deer (*Odocoileus hemionus and O. virginianus*) used this area occasionally. Densities of moose and elk in Elk Island National Park during the late 1970's were around nine to ten animals/km² (Bishoff 1981). The stocking rates of these species at the MWRS were up to three times as high (Table 2.1). Supplementary winter feeding of the semi-domesticated ungulates using the quarter section was a common practice.

The surrounding sanctuary, on the other hand, was subject to a grazing system with "natural" densities of wild moose and deer. Very few wild elk have been sighted in this area. In addition to the early land use history which involved partial clearing and cattle grazing from the mid 1920's until the early 1970's, the major difference between the two grazing systems during the most recent period was the larger number of elk and bison utilizing the NW quarter section.

3.2 Methods

3.2.1 Selection of study sites

The study was focused on three plant community types: aspen forest, balsam poplar forest and tall shrub fen. Physiognomic characteristics of the stand and its topographic position were the main criteria of the selection of several sites within areas of different grazing regimes (Figure 2.2). The study area was classified into areas with high, intermediate and low levels of use by native ungulates. The heavily grazed NW quarter of the MWRS was to be compared to the bird sanctuary with its comparatively low densitiy of ungulates. The three quarter section of

the MWRS, which had shared the grazing history of the quarter to some degree, was classified as an area of intermediate grazing intensity. Reasonably large (> 1 ha) and homogenous forest stands were chosen within areas of low and high grazing intensity. Extensive tall shrub fens were absent from the quarter section. Therefore, the sites representing this community type in the quarter could only be located in the narrow bands of tall willows around slough margins.

3.2.2 Sampling procedure

After the period of rapid vegetative growth of most plant species in spring and early summer, the plant community survey was conducted during the second half of June 1983. Within each of the previously selected study sites, 2 m X 2 m quadrats were placed at random locations. The number of quadrats surveyed at each site was limited by the time available. Ten quadrats were sampled in at least one stand in every community type within a grazing regime. Five plots were surveyed in each remaining site (Table 3.1).

In each quadrat, a visual estimate of the per cent cover for each vascular plant species was recorded. The density of each species was determined by counting each shoot rooted in the quadrat. If the density was greater than 50, the shoots were counted in a representative 1 m X 1 m square in a corner of the plot. The counts were then converted to the density of a unit area (i.e. 1 m^2). As the density of graminoids, willow clumps and some prostrate plants is very difficult to measure with this method, no densities were recorded in the tall shrub fens. An estimate of the relative frequency of each species in a stand was obtained by dividing the number of quadrats in which the species was present by the total number of quadrats in the respective sites. The terminology of all vascular plant species follows the revised edition of Moss' *Flora of Alberta* (Packer 1983).

3.2.3 Ordination

For the initial analysis of community data, a method was needed which utilized all data points to summarize and visualize the relationships among samples (and among species). As no

Table 3.1: Stand characteristics of forest and shrub fen study sites.

COMMUNITY Location	Stand	species diversity (d) N	d=N/ln(area)	sample size [number of 2m x 2m plots]	minimum stand origin dates date	soil type
ASPEN FOREST						
Quarter	Potr-2	36	12.02	5	1937	orthic grey luvisol
	Potr-3	37	12.35	5		" " "
	Potr-6	45	12.20	10	1937	" " "
Sanctuary	Potr-1	36	9.76	10	1937	" " "
	Potr-5	41	11.11	10	1898 (1936)	" " "
BALSAM POPLAR FOREST						
Quarter	P-1	48	13.01	10	1937	humic luvic gleysol
	P-3	36	12.02	5		?
	P-4	31	10.35	5		?
Sanctuary	Poba-1	37	12.35	5	1937	humic luvic gleysol
	Poba-2	40	13.35	5		" " "
	Poba-4	44	11.93	10	1897 (1936)	" " "
TALL SHRUB FEN						
Quarter	Will-2	65	16.15	14	--	?
Three Quarter	Will-3	66	18.42	9	--	?
Sanctuary	Will-4	35	9.77	9	--	?

Dates in parenthesis denote origin of numerous young trees in two-phased age structures.

environmental data were collected with the community samples, the ordination of the floristic data seemed to be most appropriate for this purpose. The ordinations of per cent cover values were performed using detrended correspondance analysis (DECORANA), an ordination program developed at Cornell University, Ithaca, New York (Hill 1979). Ordination is a method for analyzing multivariate data sets. The desired result is the arrangement of samples (or species) according to their mutual similarities in a low-dimensional space (Gauch 1982). Various procedures or algorithms have been applied to calculate scores for either species or samples along a small number of axes from floristic data only (Greig-Smith 1980). DECORANA was the most recently proposed algorithm involving simple matrix algebra for eigenanalysis, rescaling and detrending of scores along the major axis (Hill and Gauch 1980). The output comprises scores for each sample (and each species) along four axes that account for most variation in the data set.

The input for the ordination program must be a species by sample data matrix. For the data matrix each quadrat was regarded as a sample. This data matrix contained information on the variability of the cover of the field layer within as well as among the stands. Two options of the computer program allow the user to manipulate the data set. The data can be transformed to any desired scale. Rare species can be down-weighted. These options were used to explore the influence of properties of the data set on the results of the ordination.

The visual cover estimate was the best available measure of a species' importance at a site. Although cover may not always be equivalent to the importance of a species in the ecosystem, this measure of plant abundance is commonly used by ecologists because it is easily obtained. However, the scale used to estimate cover in the field may be distorted by the computation procedure of the ordination algorithm if the data have a wide numerical range. The enormous range of cover values (0.01 to 100%) observed in the field may cause an overemphasis on the few species with high cover, while less abundant species have little or no influence on the computations. In order to ensure that all species have some impact on the configuration of the ordination diagram, a transformation of data with a wide range has been

recommended (Hill and Gauch 1980). The data set was transformed to the Domin scale (Appendix 1) to examine the differences in the species composition of the samples.

Species which are present in only one or very few samples may have adverse effects on the ordination (Gauch 1982). Often the sample containing the single record of a species will be located at an extreme position of an ordination diagram. Samples which have otherwise a very similar species composition, may be located at opposite ends of an axis, because the only occurrence of a species happened to be in one of these samples. This means that the ordination algorithm places a strong emphasis on extremely rare species. Whether a rare species is found in a sample is purely a matter of chance. It largely depends on the size of the sample or the sample area. Therefore, down-weighting or removal of rare species has been suggested as a means to rectify this problem (Hill and Gauch 1980). The only use of this program option was made for the ordination of shrub fen sites. Numerous rare species were only encountered in this community type.

A further step to obtain a clear, meaningful ordination diagram was to subdivide the data set into groups of similar samples determined by the previous ordination. These subsets were then further analyzed (Peet 1980). The new ordinations are not influenced by variation among these floristically very different groups. Thus, the sources of variation within the subset may become more obvious. Here, forest communities and tall shrub fens were ordinated separately.

3.2.4 Comparison of species abundances

The next step in the analysis was to break the plant communities down into their components, the plant populations. The objective was to find statistically significant differences in the abundance of vascular plant species as a result of the different grazing systems. This analysis was performed separately for each species and each community type. Per cent cover, density and frequency were regarded as measures of abundance with different ecological implications. The means of per cent cover and density of each species in stands

outside and inside the heavily grazed quarter section of the MWRS were evaluated with planned comparisons, also called contrasts (Chew 1976). As the stand means of the plant abundance measures were to be compared in a predetermined way (i.e. heavily grazed versus lightly grazed stands), this procedure allowed an increased precision of the statistical testing procedure. From the total variation of plant abundance within and among stands, only the component of variation due to differences in the grazing system could be extracted and tested for its significance. The binomially distributed frequencies had to be tested with contingency tables (Greig-Smith 1983).

3.2.5 Further stand characteristics

Although the tree canopy cover was estimated in the quadrats sampled in the forest communities, a more accurate measure of the tree overstory was sought. In most stands the basal area of trees was determined by measuring the diameter at breast height (dbh) in 15 m X 15 m plots. If time permitted, tree cores were taken of all healthy trees in these quadrats.

The air photos of the study area from the 1920's and 1950's were examined to get clues to the stand origins and the fire history of the sanctuary. Wedges or disks of balsam poplar with fire scars were collected from various locations with additional tree cores. Wedges, disks and cores were analyzed in the laboratory.

A brief inspection of the soils was carried out in most stands. A shallow soil profile was described and the soil type was determined according to the Canadian System of Soil Classification (Canada Soil Survey Committee 1978).

3.3 Results

3.3.1 Ordination

The ordination of all quadrats showed a clear pattern (Figure 3.1). Aspen and balsam poplar forests were separated according to their location inside or outside the MWRS. A single

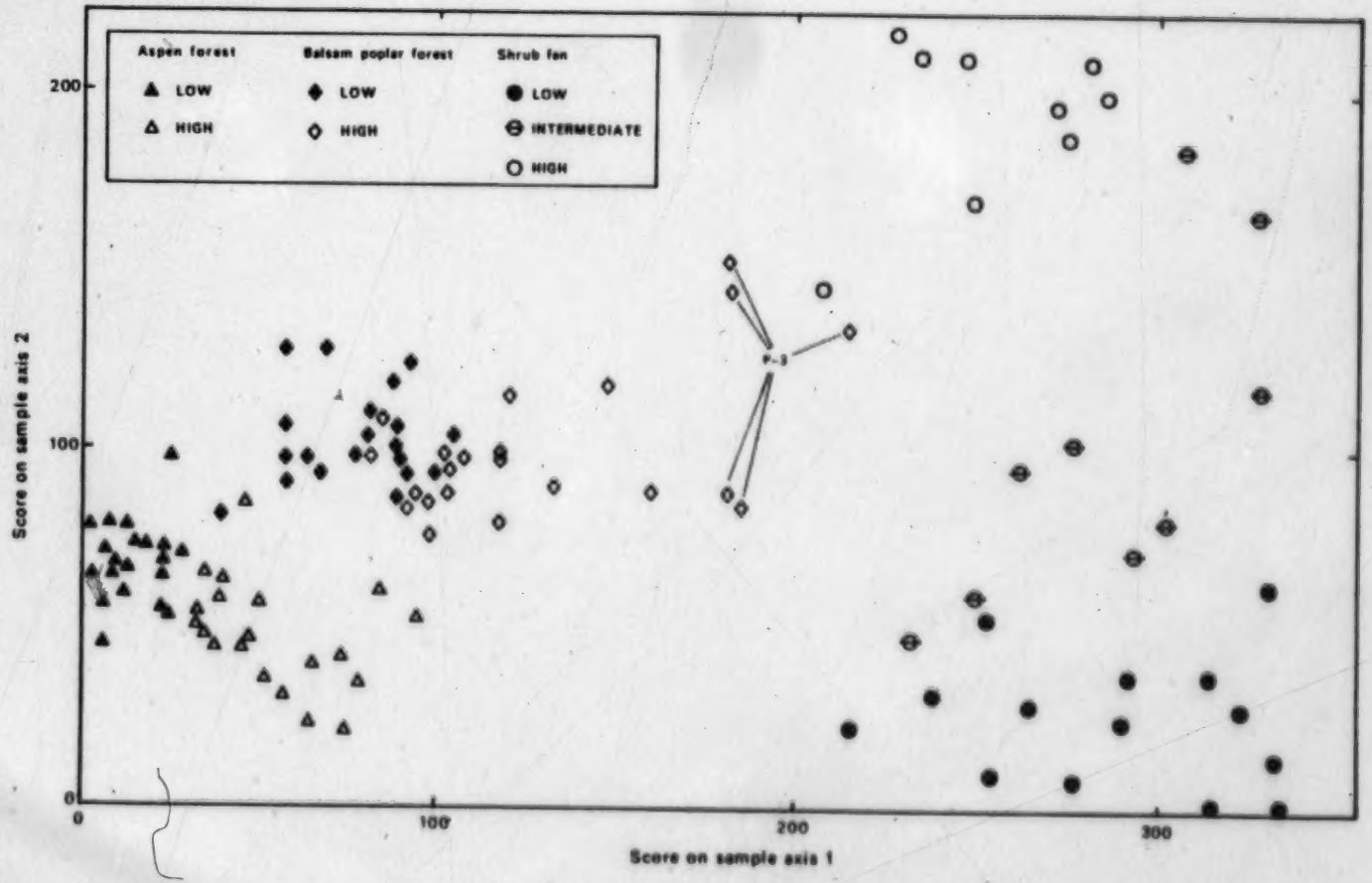

Figure 3.1: Ordination diagram of the total vascular plant cover in sample quadrats from the aspen forest, balsam poplar forest and shrub fen sites in relation to low, intermediate and high grazing intensities.

balsam poplar forest stand (P-3) formed an exception as it lay much closer to the willow sites. Disregarding this site, the samples of the aspen as well as those of the balsam poplar forest were closely packed. The three tall shrub fen sites were arranged along the second axis. The samples of this community type were much more dispersed in the ordination diagram than the forest sites. This indicates that the variation in the species composition of the shrub fen samples was much greater than in the forest stands.

Forest and tall shrub fens were analyzed separately. The atypical balsam poplar stand (P-3) was excluded from these ordinations, because it was near the willow sites. The ordination of transformed cover values of forest quadrats again showed an arrangement of community types along the first axis (Figure 3.2). The samples from aspen forest sites outside and inside the enclosure of the MWRS were well distinguished by the second axis. There was slightly more overlap within the balsam poplar forest stands subjected to the different grazing systems.

The tall shrub fen species with very low frequency (less than four occurrences in all stands) were excluded from the data set. In the ordination diagram (Figure 3.3), samples from the sanctuary formed a distinct group at one end of the first axis. The remaining two sites were also separated to some degree at the other end of this axis.

3.3.2 Species abundance comparison

The results of the analysis of differences in species abundances under different grazing intensities are shown in Tables 3.2 and 3.3. The plant species were classified according to their pattern of abundance change. Species with a significantly higher abundance in the quarter section were called increasers, species with a lower abundance at high grazing levels were denoted as decreasers. Two separate analyses were performed for the balsam poplar forest with and without the atypical site P-3. Species which showed significant differences in both cases are shown in the table only. Very few differences were found to be caused by the exclusion of the samples of the stand P-3.

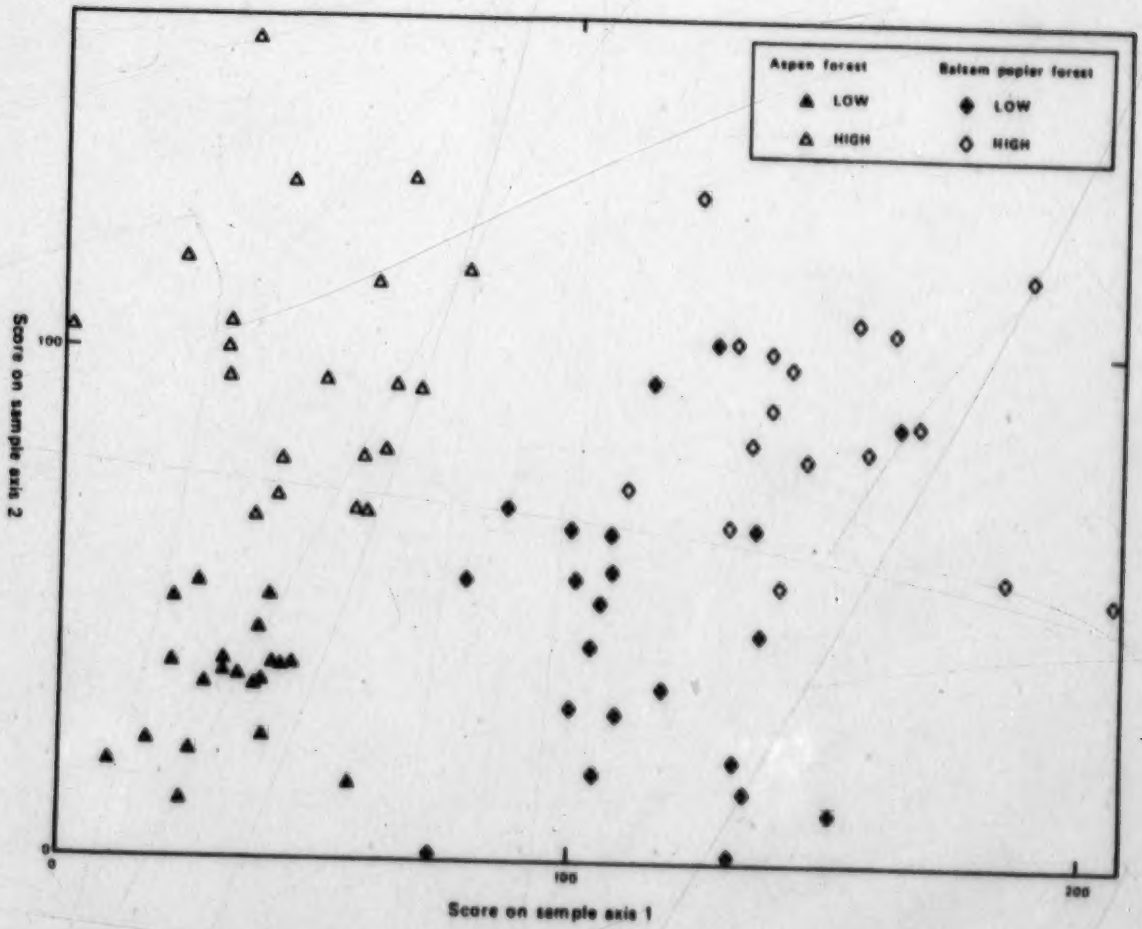

Figure 3.2: Ordination diagram of the total vascular plant cover in the sample quadrats from the aspen and balsam poplar forest stands (without stand P-3) in relation to low and high grazing intensities.

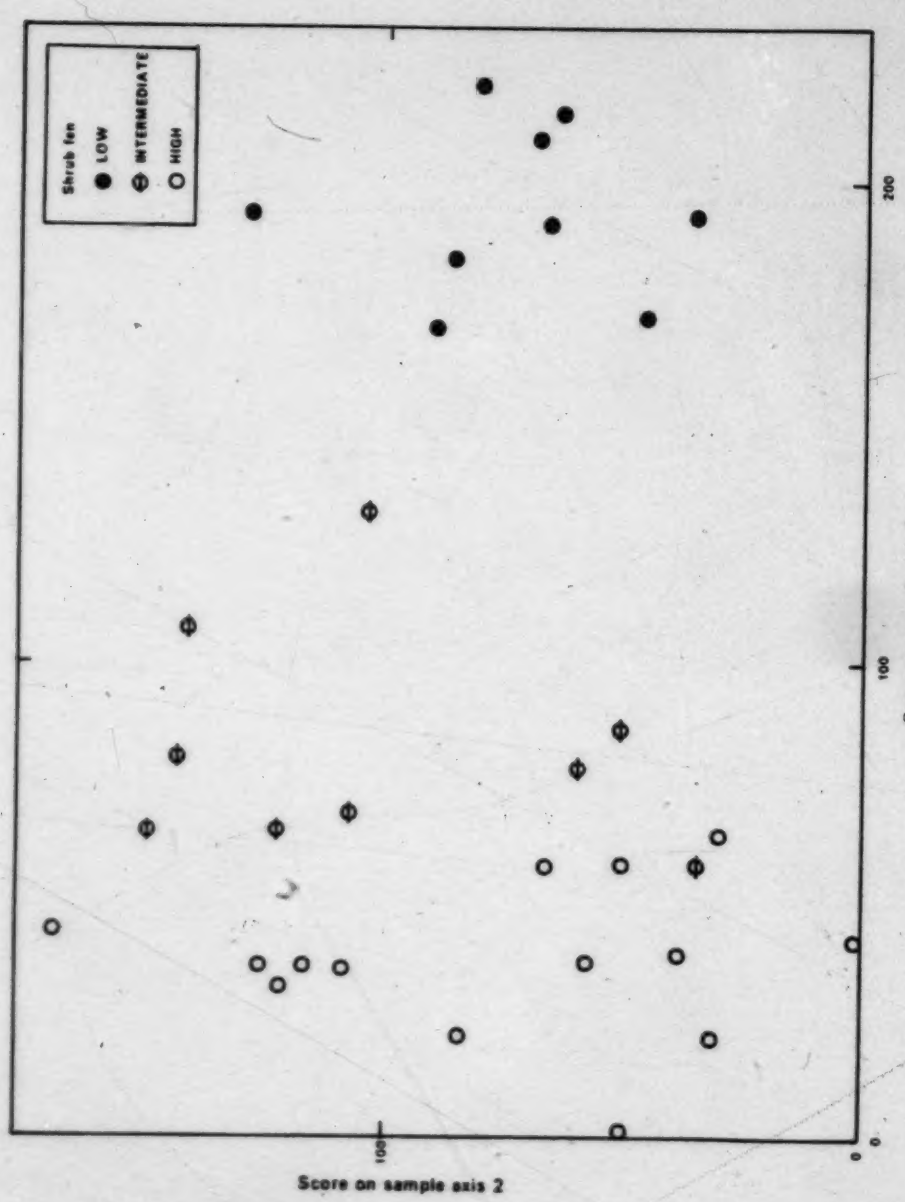

Figure 3.3: Ordination diagram of the total vascular plant cover in sample quadrats from the shrub fen sites with low, intermediate and high grazing intensities.

Table 3.2: Comparison of per cent cover (C), density (D) and relative frequency (F) of vascular plant species in the aspen forest stands.

RESPONSE CATEGORY		LIGHTLY GRAZED SANCTUARY		HEAVILY GRAZED QUARTER		SIGNIFICANCE
Species	abundance measure	mean N=20	standard error	mean N=20	standard error	*** P<0.005 ** P<0.01 * P<0.05
DECREASERS						
Shrubs: *Viburnum edule*	C	1.11	0.24	0.26	0.10	***
	D	4.85	0.69	0.85	0.23	***
	F	0.35	--	1.00	--	***
Prunus virginianus	C	1.86	0.48	0.36	0.24	**
	D	3.50	0.73	0.50	0.26	***
	F	0.55	--	0.20	--	*
Amelanchier alnifolia	C	3.31	0.75	1.42	0.42	*
	D	9.10	2.13	3.55	0.99	*
Lonicera dioica	C	0.92	0.25	0.27	0.15	*
	D	5.30	1.59	1.60	0.72	*
Forbs: *Aralia nudicaulis*	C	10.00	1.11	1.80	0.34	***
	D	20.95	1.58	3.85	0.70	***
	F					
Epilobium angustifolium	C	0.77	0.13	0.00	--	***
	D	4.40	0.78	0.00	--	***
	F	0.85	--	0.00	--	***
Disporum trachycarpum	C	0.77	0.16	0.31	0.09	*
	D	9.00	0.61	1.10	0.36	***
	F	0.80	--	0.45	--	*
Maianthemum canadense	C	1.35	0.30	0.98	0.22	**
	D					
Petasites palmatus	D	4.45	1.03	1.55	0.82	*
Aster conspicuus	F	0.55	--	0.20	--	*

Table 3.2 - continued.

RESPONSE CATEGORY		LIGHTLY GRAZED SANCTUARY		HEAVILY GRAZED QUARTER		SIGNIFICANCE
Species	abundance measure	mean N=20	standard error	mean N=20	standard error	*** P<0.005 ** P<0.01 * P<0.05
INCREASERS						
Shrubs: *Rubus idaeus*	C	0.05	0.05	1.86	0.53	*
	D	0.20	0.19	7.90	1.85	***
	F	0.05	--	0.80	--	***
Corylus cornuta	C	21.55	3.17	30.60	3.08	*
	D	17.65	2.03	35.70	3.14	***
Symphoricarpos albus	C	1.04	0.29	3.61	0.85	*
	D	5.40	0.85	11.80	1.36	***
Rosa acicularis	D	5.85	0.97	10.9	1.45	**
Ribes oxycantholdes	F	0.00	--	0.35	--	*
Forbs: *Taraxacum officinale* (I)	C	0.01	0.01	0.07	0.01	***
	D	0.10	0.06	1.85	0.45	***
	F	0.10	--	0.70	--	***
Lathyrus ochroleucus	C	1.27	0.17	1.17	0.18	*
	D	8.80	1.01	16.25	2.00	*
Fragaria virginiana	D	4.70	1.18	12.25	2.92	*
Oryzopsis asperifolia	F	0.10	--	0.45	--	*
INTRODUCED (but not significant)						
Poa spp.	F	0.00	--	0.40	--	n.s.

(I): Introduced species significantly more abundant in the quarter section.

Table 3.3: Comparison of per cent cover (C), density (D) and relative frequency (F) of vascular plant species in the balsam poplar forest.

RESPONSE CATEGORY		LIGHTLY GRAZED SANCTUARY		HEAVILY GRAZED QUARTER		SIGNIFICANCE
Species	abundance measure	mean N=20	standard error	mean N=20	standard error	*** P<0.005 ** P<0.01 * P<0.05
DECREASER						
Shrubs: *Viburnum edule*	C	0.41	0.20	0.00	--	*
	D	0.55	0.28	0.00	--	*
Lonicera involucrata	F	0.85	--	0.45	--	*
Forbs: *Aralia nudicaulis*	C	19.90	2.68	2.01	0.59	***
	D	20.90	1.49	3.05	0.94	***
	F	1.00	--	0.50	--	***
Epilobium angustifolium	C	1.83	0.30	0.00	0.00	***
	D	7.45	1.37	0.03	0.06	***
	F	0.95	--	0.10	--	***
Disporum trachycarpum	C	0.52	0.14	0.01	0.01	**
	D	1.75	0.38	0.30	0.21	**
	F	0.65	--	0.15	--	***
Maianthemum canadense	C	1.07	0.31	0.26	0.05	**
	D	12.40	3.49	1.93	2.12	**
	F	0.50	--	0.15	--	*
Rubus pubescens	C	3.76	0.62	0.96	0.26	**
	D	19.40	3.15	5.40	1.18	**
Pyrola asarifolia	C	0.32	0.17	0.06	0.05	*
	D	4.65	1.48	1.00	0.91	*
Heracleum lanatum	C	3.40	0.65	0.85	0.24	*

Table 3.3 - continued.

RESPONSE CATEGORY		LIGHTLY GRAZED SANCTUARY		HEAVILY GRAZED QUARTER		SIGNIFICANCE
Species	abundance measure	mean N=20	standard error	mean N=20	standard error	*** P<0.005 ** P<0.01 * P<0.05
INCREASERS						
Shrubs: *Rubus idaeus*	D	1.85	1.62	7.85	2.81	**
	F	0.70	--	1.00	--	*
Ribes oxycanthoides	D	7.70	0.62	24.65	1.59	*
Forbs: *Galeopsis tetrahit* (I)	C	0.01	0.01	2.66	0.62	*
	D	0.07	0.05	37.35	237.61	*
	F	0.05	--	0.75	--	*
Calamagrostis canadensis	C	0.03	0.01	0.59	0.18	**
Taraxacum officinale (I)	D	0.25	0.10	1.60	0.41	*
	F	0.20	--	0.60	--	*
Viola canadensis	D	0.55	0.36	5.50	2.78	*
Pteridophytes:						
Equisetum arvense	C	0.10	0.05	0.49	0.13	*
	D	3.15	0.68	18.25	5.64	*
INTRODUCED (but not significant)						
Urtica gracilis (I)	F	0.00	--	0.45	--	n.s.

(I): Introduced species significantly more abundant in the quarter section.

For the shrub fen community only two sites were examined for differences in species abundances. The site in the three-quarter section (Will-3) was excluded from the analysis, because it has its own unique grazing history. The remaining two sites were tested for differences in frequencies only (Table 3.4). A detailed analysis of cover was not carried out, because the ordination diagram (Figure 3.3) showed large variation in species composition between the sites as well as among the individual quadrats. The lack of replicative sites for the two grazing systems made a statistical evaluation of differences impossible (Hurlbert 1984). As only one site was sampled in each grazing system, the variation of plant abundance among sites of the same grazing system could not be statistically evaluated. Therefore, the observed variation between the two sites may not necessarily be a result of different grazing regimes.

3.3.3 Stand characteristics and fire history

Basal area and density of trees forming the forest canopy are shown in Table 3.5. Very few balsam poplar were recorded in the aspen stands. In contrast, aspen were encountered frequently in the lowland forest. Whereas the upland forest canopy may be purely aspen, the balsam poplar lowland forest usually has a variable mixture of the two poplar species (ranging from 20% to almost 100% balsam poplar).

Frequency distributions of dbh and age of both tree species in several stands are shown in Figures 3.4 and 3.5. All stands were even-aged with almost all trees originating between 1937 and 1940. In some stands a few much older trees were found. There was no apparent correlation between age and size of trees, as a wide range of sizes is commonly present in even-aged trees (Moss 1932). The size structures of aspen stands were similar. Again the dominance of aspen was obvious. In the balsam poplar stands proportions of aspen and balsam poplar varied. It seems that balsam poplar grew to a larger size than aspen within the same time span and at the same site.

The evidence for a complex fire history of the study area was derived from many sources. The occurrence of fires could be dated directly with fire scars on trees. Balsam poplar

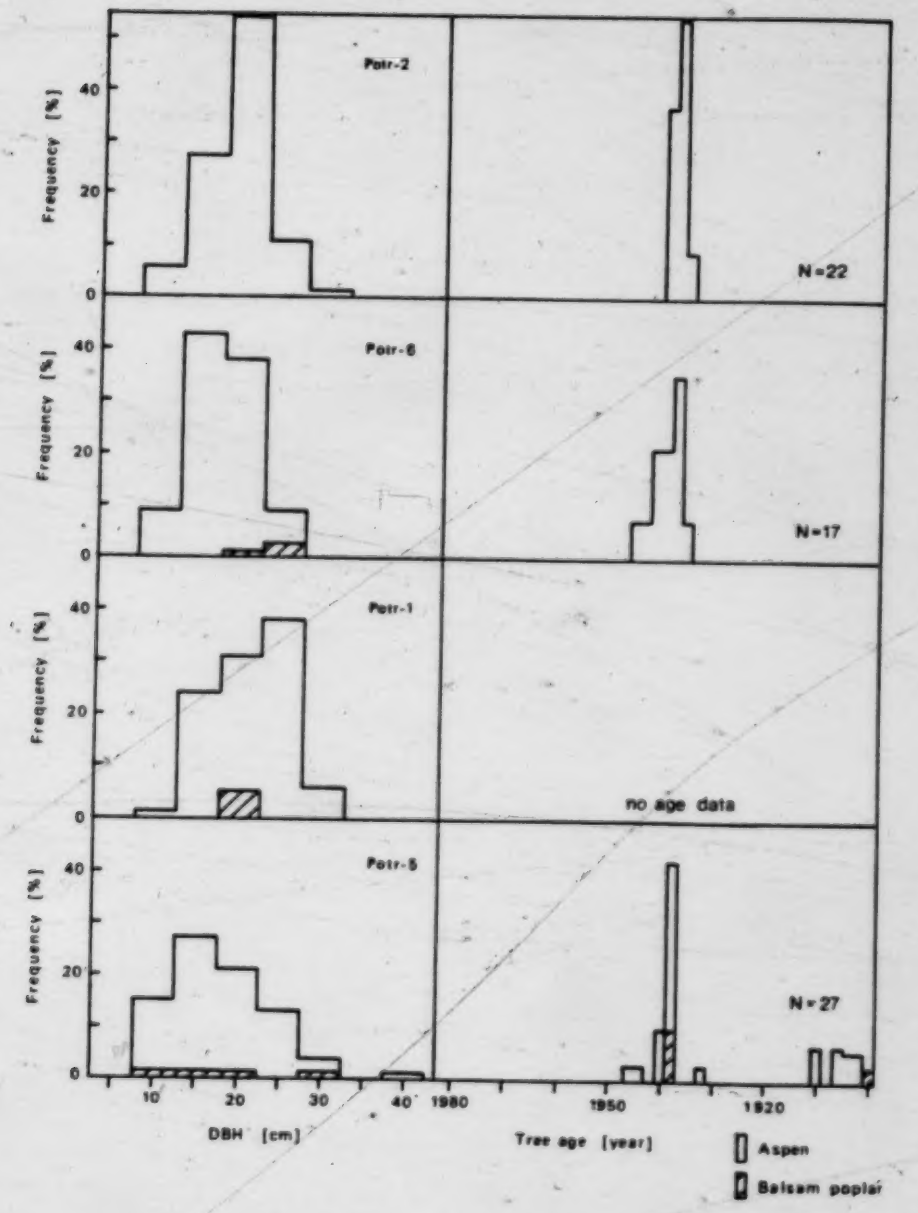

Figure 3.4: Size and age structure of trees in the aspen forest stands.

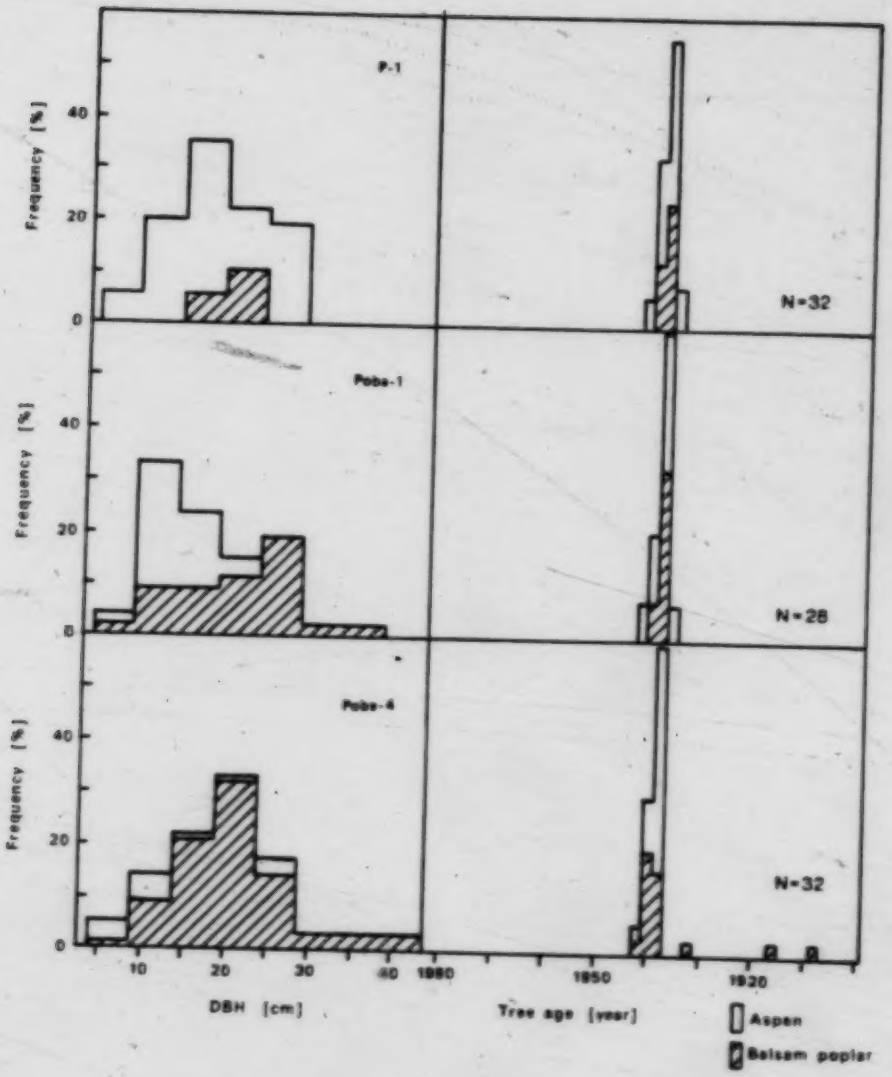

Figure 3.5: Size and age structure of trees in the balsam poplar forest stands.

Table 3.4: Comparison of relative frequency (F) of vascular plant species in the shrub fen community.

RESPONSE CATEGORY	LIGHTLY GRAZED SANCTUARY	HEAVILY GRAZED QUARTER	SIGNIFICANCE
Species	Will-2 N=9 F	Will-4 N=14 F	*** P<0.005 ** P<0.01 * P<0.05
DECREASERS			
Forbs: *Cornus canadensis*	0.00	0.44	*
Epilobium angustifolium	0.14	0.78	**
Galium triflorum	0.21	0.89	**
Mentha arvense	0.07	0.78	***
Mertensia paniculata	0.00	0.89	***
Petasites sagittatus	0.07	0.89	***
Rubus arcticus	0.21	0.78	*
Pteridophytes: *Equisetum arvense*	0.14	0.78	**
INCREASERS			
Shrubs: *Salix pyrifolia*	0.79	0.00	***
Forbs: *Aster borealis*	0.71	0.11	*
Fragaria virginiana	0.86	0.00	***
Parnassia palustris	0.50	0.00	*
Sonchus arvensis (I)	0.93	0.00	***
Taraxacum officinale (I)	0.93	0.00	***
Poa palustris (I)	0.86	0.11	***
Carex aurea	0.71	0.00	***

(I): Introduced species significantly more abundant in the quarter section.

Table 3.5: Relative basal area and density of trees (>2cm dbh) of aspen and balsam poplar stands (measured in 15m x 15m plots).

COMMUNITY Location	Stand	*Populus tremuloides* density	*Populus tremuloides* %basal area	*Populus balsamifera* density	*Populus balsamifera* %basal area	Total density	Total %basal area
BALSAM POPLAR FOREST							
Quarter	P-1	25	0.28	16	0.15	41	0.43
Sanctuary	Poba-1	21	0.12	25	0.38	46	0.50
	Poba-4	6	0.04	33	0.53	39	0.57
ASPEN FOREST							
Quarter	Potr-2	66	0.46	0	0.00	66	0.46
	Potr-6	64	0.36	3	0.03	67	0.39
Sanctuary	Potr-1	40	0.40	2	0.01	42	0.41
	Potr-5	33	0.36	2	0.02	35	0.38

with multiple fire scars are not uncommon in lowland forests of the study area. However, it was difficult to find well-preserved trees for age studies. Only on one balsam poplar from the stand Potr-5 could the dates of fires be determined accurately. The scars recorded four fires in the years 1929, 1936, 1941 and 1946. The approximate fire dates from two other tree disks appeared to agree with these dates. Fires on the Cooking Lake Forest Reserve in 1924 and in 1929 were mentioned by Stefiszyn (1983). K. Williams, the retired warden of the bird sanctuary, remembered that the last major fire in the Ministik area raged in 1946 or 1947 (pers. comm. - Isabel Simons).

Air photos represented another source of information. Oblique air photos of the study area from 1924 (CA 90,37-40; CA 91,13-14) showed that the whole area had been recently burned over. The uplands were bare or covered with scrub. Some trees in the lowlands had obviously survived the fire(s). Vertical air photos from August 1950 (AS-138 5306,79-81) show that much forest cover had reestablished in the northern half of the sanctuary. Areas in the southwest part (Figure 2.2) were covered with much smaller aspen or balsam poplar saplings. These had probably started to grow after the last fire of 1946. The northwest part of the sanctuary appeared to have been burned only partially. The remaining area of the sanctuary including the MWRS seemed to have largely escaped from this fire or it was only subject to a low intensity surface fire.

The final evidence of forest fires stems from the tree age structures (Figures 3.4 and 3.5). The vast majority of trees seem to have originated after the the fire in 1936. Most stands are nearly even-aged. No regeneration of aspen or balsam poplar has occurred in the forest sites in the last 35-40 years. In a few stands some older trees were encountered. Fire scars on live trees demonstrate the potential of poplar to survive forest fires. No trees predating the fires of 1892 and 1895 were discovered in the study area. The oldest tree was 84 years old.

It must be assumed that the fire record from a single tree is not complete. Nevertheless, it can be concluded that fires were not uncommon in the study area until 1946. Most forests had almost 50 years to recover. The tree overstory of the Ministik Bird Sanctuary seems to have

originated after two major fires in 1936 and 1946. All study sites were located within the area of the older forest.

3.4 Discussion

3.4.1 Ordination

The first ordination techniques were developed by researchers who viewed vegetation as a continuum of variation rather than a mosaic of discrete plant communities (e.g. Curtis and McIntosh 1951, Whittaker 1956). This continuum concept suggested that the abundance of species is largely controlled by environmental gradients (Whittaker 1967). As the abundance of various species may vary independently along the gradient a firm definition of plant associations was questionable (Gleason 1926). Consequently, ordination techniques were developed to arrange samples of vegetation in a coordinate system so that distances between sample locations would represent and visualize their similarity or dissimilarity (Gauch 1982). It is important to note that the idea and methodology of ordination do not depend on a continuous variation in vegetation composition (Greig-Smith 1983).

Initially these methods were limited by much subjective judgement through *a priori* postulation of the major environmental gradients and the application of rather arbitrary species weightings. With the advent of powerful electronic computers, more sophisticated techniques were developed in the 1960's and 1970's. They have the advantage that subjectivity can be reduced to a large extent (Gauch 1982). The species-sample matrix represents a multivariate data set where each species and each sample may be regarded as a variable. Each sample can be viewed as a point in a multidimensional space defined by axes representing the abundance of each species in the data matrix (Ramensky 1930). The aim of modern ordination techniques is to reduce this hyperspace to a few dimensions which account for a maximum of the variation and which can be readily visualized (Dale 1975). Complex computations are necessary to perform this task. If the same procedures are applied to species located in a hyperspace defined

by sample axes, the result is an ordination diagram showing species with similar distributions in the samples. Some of the important ordination procedures, principal component analysis (PCA), reciprocal averaging (RA) and an improved version called detrended correspondence analysis (DECORANA) have recently been described and evaluated by Gauch (1982).

The step from high to low dimensional space is often obscured by complex calculations carried out by the computer. The researcher is left with the task of interpreting the ordination diagrams. Ordinations of artificial data sets have revealed some properties (and problems) of the ordination techniques (e.g. Gauch and Whittaker 1972,1976; Gauch 1982). The comparison of various techniques applied to artificial and real data suggest that RA and DECORANA are quite effective in reproducing real relationships among samples (Oksanen 1984). It has been pointed out that manipulations of the data (e.g. transformation, down-weighting or elimination of rare species and/or atypical samples) may improve the ordination significantly (Hill and Gauch 1980).

As mentioned above, the interpretation of ordination diagrams and major axes may be difficult, because the calculation of scores cannot be easily grasped. An understanding of the way properties of the data set may modify the outcome of an ordination is therefore very helpful. Nevertheless, the basic problem remains to find a pattern in the diagram and to attempt to explain it. A common approach to interpret ordination diagrams is to find environmental variables which seem to correspond to the axes. If no environmental measurements were taken with the community samples, this approach involves a certain amount of subjectivity. It is the qualitative observations and knowledge of the researcher rather than quantitative measurements that provide for the identification of the ecological factor(s) causing the pattern.

The objective in the ordination exercise in this study was twofold. First, the variation within and between stands and community types was to be examined. The pattern of the distribution of the quadrats in the ordination diagram was to provide clues to the sources of the variation of plant species composition and abundance. Second, the ordination was intended to

confirm that homogeneous stands of the predefined community types had been selected. Therefore, it had to be expected that replicative stands of a community type within a grazing system would not be distinguished in the ordination diagrams.

The quadrats sampled in several stands were grouped closely together for aspen and for balsam poplar communities (Figure 3.1). This supported the initial classification as well as the further step to separately analyze the two forest community types. The proximity of the aspen to the balsam poplar quadrats on the ordination diagram (Figure 3.1), considering the much larger distance to the shrub fen quadrats, confirms that there may be similarities in their species composition. This agrees well with Moss' classification (1932) dividing the association of the poplar forests into these two consociations.

The few outliers do not disturb this clear pattern. However, the location of all samples of the stand P-3 in an intermediate position between forest and shrub fen quadrats is not likely to be a product of chance. This balsam poplar stand was sampled in a small, closed depression, whereas all other balsam poplar stands were located at the base of a slope adjacent to a larger lowland area. In this stand, unlike the others, large puddles of water were observed for many days after heavy rains. It appears that this site differed from the other balsam poplar stands in its soil properties as well as in its floristic characteristics. If this site were included in the calculations, precautions had to be taken in the comparison of cover, density and frequency differences of lightly and heavily grazed balsam poplar stands

The analysis of data transformed to the Domin scale accentuates the total species composition of each sample, because the importance values of all species have a similar magnitude. The close packing of the samples from forest communities as compared to the tall shrub fens (Figure 3.1) can be explained by a much more consistent species composition of the sample quadrats. The species diversity index (d) in the shrub fens of the MWRS is considerably greater than in the forest (Table 3.1). However, mainly the greater differences in species composition among the individual quadrats cause the wider spread of the shrub fen community type in the ordination diagram. This indicates that the sampling procedure may have been

inefficient in the shrub fen community. In order to reduce the effect of the great variation of species composition among samples, rare species (present in less than 10% of the samples) were removed for the analysis of shrub fen quadrats. However, neither down-weighting nor the elimination of rare species seemed to improve the ordination of samples to any extent.

Although they have a much larger spread, all shrub fen samples lay on one end of the first axis. The aspen forest quadrats covered the other end. The balsam poplar stands were located in an intermediate position, with the stand P-3 placed closer to the shrub fen sites (Figure 3.1). This arrangement of the three plant community types allows a straightforward interpretarion of the first axis of the diagram. It corresponds to the topographical position of the community types. Correlated to the variation in the topographical location are numerous environmental variables. Whittaker (1970) developed the concept of complex gradients. Many environmental gradients (e.g. soil moisture and soil temperature regime, nutrient status, organic matter) change through space. The pattern of change in soil types in relation to topography is a soil catena. The transition from Orthic Gray Luvisols in the upland forest to Humic Luvic Gleysols in the lowland forest and Organic soils in the shrub fens and sedge meadows represents the catena at Ministik (Table 3.1). This variation in soil types and properties with topography is largely responsible for the change in the plant community types (coenocline).

Forest and shrub fen quadrats, excluding the atypical stand P-3, were ordinated separately to clarify further patterns in the data. The first axis separates aspen from balsam poplar sites and it represents again the complex topographic gradient. The second axis distinguishes well between lightly and heavily grazed samples. This suggests that a grazing gradient is second in importance in the forest communities. Whether this is due to differences in species composition or species abundance cannot be decided from the ordination. The two axis account for only one third of the variation in the data set. As further environmental gradients were not obvious, it may well be that much of the remaining variation is due to random variation.

The separate ordination of shrub fen community showed a similar arrangement of its quadrats as in the ordination of all quadrats (Figure 3.1). Now the three sites were separated along the first axis. Although the variation between the samples was much greater than in the forest stands, the separation of the sites suggests a definite difference between them. The three sites are well arranged along the first axis according to the grazing intensity. The site in the three-quarter section (Will-3) was subject to a light to moderate grazing regime and it shares the land use history with the site in the quarter section. Although the interpretation of the first axis as a gradient of grazing intensity (and land use history) seems to be very obvious, it has to be viewed with caution. In contrast to the forest communities, no replicative sites were sampled in the three areas. In the quarter section, there simply was no other homogenous and extensive enough shrub fen site.

The interpretation of the second axis was facilitated by a comparison with the ordination diagram of all quadrats (Figure 3.1). The samples which were spread along the first axis were arranged along the second axis of the subset ordination. A soil moisture gradient could exist within the shrub fen samples. This hypothesis was confirmed by an examination of the species composition of some samples lying at the extremes of the second axis. At one end, the samples contained many species which are common in the balsam poplar forest. On the other extreme, species more characteristic of sedge meadows were recorded in the samples. Considering the small width of these shrub fen bands (commonly less than 10 m), this interpretation of the second axis points at the ecotonal nature of the sampled shrub fen sites. Unlike the larger willow-dominated depressions, these narrow willow bands between balsam poplar forest and sedge meadows are difficult to sample and to characterize, because of their transitional nature. This means that differences of species composition or abundance between sites must be investigated carefully so that they are not falsely attributed to the grazing intensity.

The close packing of forest quadrats shows that the sampling method for these communities was appropriate. The greater spread of the shrub fen quadrants indicates that the

sampling method was inadequate for this community type. A different sampling procedure, possibly a transect relating to the transitional character, should have been adopted for these willow bands.

3.4.2 Abundance changes

Prior to the discussion of plant species which seem to have different abundances in each grazing system, the actual variables describing abundance have to be looked at. Per cent cover and density are absolute measures of species abundance in a sample quadrat (Greig-Smith 1983). Both variables are related to each other through the growth habit and morphology of a particular species. The same cover value may be achieved by numerous small plants or alternatively by a few plants with a relatively large shoot area. Density is an unbound variable, as it may assume any discrete value in a sample (Smartt *et al.* 1974). Per cent cover is a bound variable (i.e. it has a maximum theoretical value) which may be the single most important measure of the ecological importance of a species (Daubenmire 1968). The larger the area a species covers, the more light it is able to intercept and to take away from other species.

Frequency of a species was determined once for an entire stand from the sample quadrats. Frequency is a measurement of the probability to find a certain species in a stand in any one trial (Greig-Smith 1983). The chance of a species being present in a sample is dependent on the size of the sample area (i.e. it is more likely to find a species in a larger sample area). Plant species with a clumped distribution may have a low frequency. However, they may have a large cover in the samples in which they are present. Such species may falsely be declared to have significantly different cover values. Thus special care must be taken in the interpretation of the statistical differences in the cover of species with non-random spatial distributions.

In each community type, plant species which have increased or decreased under high grazing pressure could be distinguished. No species showed inconsistencies in the three abundance measures. However, at times a change was only detected by one or two of the

variables. A significant decrease in cover could be a result of a smaller average size of individual plants. The reduced size may be a consequence of reduced vigor or simply an indication of foliage removal. The entire plant is only infrequently consumed (Noy-Meir 1981). Thus, the other absolute measure of abundance, the density of a plant species per unit area, should be as important for determining changes due to high grazing intensity. The problem with measuring density is the ease of distinguishing individual plants. As most species are propagated by underground stems or rhizomes it was impossible to identify the actual genets in this field survey. Consequently, clearly distinguishable shoots were counted in this study. For some species their growth form rendered this difficult (e.g. *Ribes* spp., *Lonicera involucrata, L. dioica, Symphoricarpos* spp., *Rubus pubescens, Fragaria* spp.). For others no attempt to measure density was made (e.g. *Salix* spp., Graminoids), because an enormous amount of time would have been necessary to generate useful data.

The results of the abundance comparisons (Table 3.2 and 3.3) showed that a few species had parallel changes between the aspen and the balsam poplar forests. This is a significant indication that similar forces must be affecting both communities independently from the complex environmental gradient that exists between them.

Three broad-leaved species (*Aralia nudicaulis, Disporum trachycarpum, Epilobium angustifolium*) of the tall herb stratum are much more abundant in the sanctuary. These relatively conspicous plants may be consumed frequently by ungulates foraging in the forest during the growing season. Nietfield's data (1983) showed that elk selected for *A. nudicaulis* during August. This grazing pressure reduced the actual number of plants as is shown by significant density decreases.

Two species of the shrub layer have increased under the greater grazing intensity (*Rubus idaeus, Ribes oxycanthoides*). Both species have protective spines or bristles and may, therefore, be avoided by ungulates. The density increase of wild rose (*Rosa acicularis*) in the aspen forest stands in the quarter section may be explained in the same way. Gates (1980) reported that wapiti never fed on rose and raspberry during the winter. The forage selectivity of

ungulates provides an advantage for the avoided plant species. The reduced competition with major forage species allows an increase of avoided plants.

Some preferred forage shrubs like *Amelanchier alnifolia*, *Prunus virginiana* and *Viburnum edule*, characteristic for the aspen forest have decreasded in abundance. The dominant shrub of this community type, *Corylus cornuta*, has increased slightly. *Symphoricarpos albus*, a low growing, hardy shrub, increased as well. *Heracleum lanatum* is a large herbaceous species common in balsam poplar stands. Only the cover of this species has decreased significantly. Some of the large and conspicous leaves of this species had been consumed in the quarter section.

A few species of the lower herb stratum have decreased (e.g. *Pyrola asarifolia, Maianthemum canadense*). This was probably caused by trampling and the creation of trails by the ungulates rather than being a direct effect of increased grazing intensity, because these species seem not to present an important part of ungulate diets. The decrease of these species may in turn allow the increase of others (Ellison 1960) such as graminoids (*Calamagrostis canadensis, Oryzopsis asarifolia*) and *Equisetum arvense*.

There are a number of introduced plant species which have been recorded mainly in the quarter section. *Taraxacum officinale*, the common dandelion, was frequently found in the forest communities. Others were less often encountered, but they all were more abundant in the MWRS. Such species were *Cirsium arvense, Urtica gracilis, Trifolium repens, Poa* spp.

Cornus stolonifera, a species characteristic of the balsam poplar forest at Ministik, has been reported to be a highly preferred forage shrub (Gates 1980, USDA 1962). This species is very susceptible to browsing as it suffers even from light to moderate use (Aldous 1952, Ross *et al.* 1970). Throughout the study area, *C. stolonifera* was not abundant in the forest stands (less than 2% cover - Appendix 2). In the entire study area, the terminal portions of the stems of this species were severely hedged due to repeated heavy browsing. It may be concluded that the growth of this shrub was limited by the wild ungulate population in the sanctuary.

It has been documented that heavy browsing pressures prevent the encroachment of grasslands by aspen and balsam poplar (Bouckhout 1971, Milner 1977). From this study at Ministik, this effect cannot be evaluated because only homogeneous forest stands were surveyed. However, it was observed that aspen and balsam poplar saplings at the forest edges in the quarter section showed signs of heavy browsing. Within the forest stands, a few suckers but no saplings were found. Under the closed forest canopy, no regeneration of aspen or balsam poplar took place.

Most studies of the effects of grazing on plant communities have been conducted in range lands of the western United States and in the Canadian prairies. In a review of such studies, Ellison (1960) discussed the ecology of range plants with respect to four categories: increasers, decreasers, invaders and non-responders. Increasers are species which initially increase in abundance with grazing intensity. They reach a maximum and drop off if grazing pressures exceed a critical value (Dyksterhuis 1949). As a direct consequence of this theoretical response pattern, similar abundances do not necessarily represent equal grazing intensities. Therefore, it can be difficult to identify increaser species if a wide range of grazing intensities is not available for the investigation. Decreaser species are characterized by a reduction in abundance under grazing pressure. Invader species take over at very high grazing levels replacing decreasers and increasers. Plants which have been introduced may belong in this class.

The four response categories can be applied to forest communities. However, studies of the changes in forest communities due to grazing by large herbivores are rare. Marks (1942) and Steinbrenner (1951) evaluated the effects of grazing on herbs in Wisconsin forest communities. Weatherill and Keith (1969) studied the effects of livestock grazing within upland aspen forests in the Rochester district of central Alberta. The grazing pattern of livestock is very different from native browsing herbivores. Cattle and horses spend only five months of the summer on the pasture. In addition to the different foraging habits, the winter use of woody perennials does not occur. Differences in the response of shrubs to grazing by livestock and native ungulates can be expected.

R. acicularis, S. albus and R. idaeus have been classified as decreaser species by Weatherill and Keith. At Ministik these shrubs had significantly increased abundance values. It is not clear whether this striking difference is an affect of the animal species foraging on the shrubs. The response of the herbaceous understory corresponds very well to the results from Ministik.

C. cornuta, the dominant shrub of the aspen forest at Ministik, could not be classified by Weatherill and Keith. It showed a contradictory response pattern in frequency and cover. In a study of the effect of a long-term exclusion of ungulates in a red pine (*Pinus resinosa*) forest, Ross *et al.* (1970) found that *Corylus* spp. had increased in density under a light grazing pressure, but it had decreased at high levels of grazing intensity. Clearly, *C. cornuta* then belongs into the increaser category, which corresponds well to its response pattern at Ministik where its density in the heavily used quarter was twice that of the sanctuary (Table 3.2).

Density of plants was not recorded in the tall shrub fen sites because graminoids and willows dominated this community type. A greater species diversity was calculated for the site in the one quarter section (Table 3.1). Many species were found in only a single or in very few quadrats. Without replicated sites, it is impossible to attribute changed species abundance to a grazing gradient. The observed differences in species frequencies (Table 3.4) could be an effect of an unknown environmental difference between the two sites. A striking difference between the shrub fen sites was the higher species diversity in the quarter section. This community type is characterized by a dense cover of sedges and grasses among the willow clumps. Nietfield (1983) reported that elk forage heavily on these graminoids at various times of the year. The reduced graminoid cover may in turn allow the growth of species which are normally suppressed or absent from this habitat type.

3.5 Conclusion

The ordinations confirmed that a complex environmental gradient related to topography was the major source of variation in the vegetation of the study area. It is important to note, however, that a grazing gradient seemed to be a second major source of variation within the plant communities studied. These conclusions were based on qualitative observations in the stands and an intuitive interpretation of the ordination diagrams. However, the clear and consistent segregation of quadrats in different community types and different grazing systems provides good evidence for the two gradients.

Differences were found between the predefined community types. The dense clusters of both forest types demonstrated that the stands sampled inside and outside the quarter section, with a single exception, formed relatively uniform community types. The shrub fen community was less clearly defined floristically, partly due to its largely ecotonal nature. Therefore, it was justified to test for differences of importance values of plant species between forest stands under different grazing regimes. Results of such an analysis for shrub fen sites had to be interpreted very carefully.

The analysis of abundances of each species in relation to the grazing systems provided evidence for increasing and decreasing species. Two groups of species with lower abundance in the quarter section were a few broadleaved herbs and some highly palatable shrubs. Several spiny or bristly shrubs had higher abundances in the forests of the quarter section. A second group of increasers with generally low abundance were ruderal species. The occurrence of these species marked the only difference in species composition of the two grazing systems. No native plant species had become extinct in the quarter section. This illustrated that the species were either very resistant or that grazing pressures had not been extreme for a long enough period of time. All other differences were changes in abundance only.

In the plant community survey, plant species which had significantly lower or higher abundances with respect to the grazing system were identified. However, the evidence for the causes of the differences in abundance was largely circumstantial. Considering the 50 years of

grazing history in the quarter section, it cannot be assumed that the differences were merely a result of the seven years of game farming. Only detailed comparative studies of the population dynamics of increaser or decreaser species may provide the information needed to explain their response pattern.

The effect of these changes was a decline in the availability of some forage plants. This may decrease the diet quality for the ungulates. It must be stressed, that changes in abundance may not be the only consequence of high grazing pressures. The change of annual forage production of selected shrub species will be examined in the next chapter. The definite change in the morphology (e.g. hedging) of some woody plants due to browsing may greatly reduce the accessibility of new growth. The effect of changes in physiognomy were difficult to quantify. A further factor to study is the existence of a grazing gradient within the quarter section. The ungulates tend to aggregate and feed close to the station. Different grazing pressures may, therefore, be observable in relation to the distance from the station.

4. The productivity of the shrub layer in relation to two grazing systems

4.1 A simulated browsing experiment

4.1.1 Introduction

The shrub layer in boreal forest communities can be a major forage source for native herbivores. In the winter after deciduous leaves have fallen and herbaceous plants have died back, the shrub stratum as a distinct physiognomic unit becomes very conspicuous. During the cold season, shrubs extending beyond the snow cover present easily accessible plant material, the principle winter food for browsing native ungulates (Telfer 1978). The frequency and the spatial distribution of shrub species in a given area partly determine the quantity and quality of the winter forage resource. The amount of available winter forage is also a function of the shrub productivity.

Numerous factors influence the annual biomass increment of woody perennials. The relative growth rate can vary widely among species (Grime and Hunt 1975) and individual plants (Burden and Harper 1980). Climatic (Nilsson and Eckersten 1983) and site quality factors (Garrison 1953) can also have a major impact on shrub productivity. These factors were of minor interest in this study. The response of shrub productivity to browsing was to be the focus. Consequently, attempts had to be made to eliminate or to account for other sources of variation.

The measurement of shrub annual net production is a difficult undertaking because secondary stem and branch growth as well as root growth can not readily be estimated (Whittaker and Marks 1975). Among wildlife biologists, it is customary to replace total shrub productivity with the production of current annual growth. The current annual growth of a shrub are all the new twigs which have extended from buds during the most recent growing season. This readily sampled component of shrub production provides reasonable estimates of winter forage production since ungulates rarely feed on the older branches and bark of shrubs

(Hunter *et al.* 1979). Leaf biomass, a second component of total annual shrub growth is also easily measured. In addition to its importance as summer forage, leaf biomass provides an estimate of the photosynthetic capacity of individual shrubs (Miquelle 1983).

The layout of the MWRS provided an opportunity to compare shrub productivity in two grazing systems. However, the history of browsing intensity could not be determined on individual shrubs. To demonstrate the relationship between productivity and browsing intensity, a clipping experiment was conducted on unbrowsed shrubs in the sanctuary. Beaked hazel, *Corylus cornuta*, was the dominant shrub species of the upland forest communities. *C. cornuta* has not been reported to be a preferred forage shrub for any native ungulate species. However, it is a principal forage shrub for browsing ungulates in the quarter section because it is very abundant. Another reason for the choice of this species was the relative ease with which the clipping treatments could be applied to the numerous unbrowsed stems of this species. The experiment was conducted in a single stand over a single season to reduce the effects of climatic and site quality factors on shrub productivity.

4.1.2 Methods

The stand Potr-1 in the Ministik Bird Sanctuary (Figure 2.2) was selected for the experiment. Initially a generalized randomized complete block design (Addelman 1969) was chosen because it provides reasonable precision (Steel and Torrie 1980). Three points were located randomly in the stand. From each point, four further points were determined. These four points were at a distance of five meters to the original spot in the four main compass directions. The ten nearest stems of *C. cornuta* were selected and tagged if they exceeded an arbitrary size (i.e. 6 mm basal diameter) and if they did not show any signs of previous browsing. In this manner a total of 120 stems of *C. cornuta* were tagged at three different locations within the stand. These locations represented the blocks of the experimental design.

In each block, four treatments were replicated on ten stems. The four treatments consisted of removing 25%, 50%, 75%, or 100% of the current annual growth of the summer of

1982 by clipping. These percentages were achieved by clipping 1/4, 1/2, 3/4 or all of the new twigs within visually estimated twig size classes. The treatments were selected to simulate different intensities of winter browsing. The clipping was done during the third week of March, 1983. *C. cornuta* was the only species studied. Other shrub species like *Amelanchier alnifolia, Cornus stolonifera* and *Salix* spp. were severely browsed in the sanctuary, which precluded them from a simulated browsing experiment.

At the end of the 1983 growing season, in the last week of August, the biomass production of the treated shrubs was measured. Leaf biomass and current annual growth served as indicator variables for productivity. All the leaves and the new twigs of 1983 were collected. The dry-weight of leaves and current annual growth was determined in the lab. Measurements of basal diameter and height of each stem were obtained in the field. Untreated control specimens from this stand were obtained in conjunction with a biomass study to be described in a later section (4.2.2.1). The control shrubs were sampled independently from the block design.

An analysis of variance was the first step in the statistical evaluation of the productivity data. The increase of productivity with shrub size was expected to be a major source of variation. Two statistical methods were available to adjust for size effects. An analysis of covariance was computed for leaf biomass and current annual growth. A requirement of this procedure is the homogeneity of the regression coefficients for all treatments. This basic assumption of analysis of covariance was tested (Steel and Torrie 1980).

The second method applied to adjust for size effects was a multiple regression analysis. A statistical model was developed to predict shrub productivity from size and clipping intensity as independent variables. As the response of productivity was expected to be non-linear, a polynomial model was chosen. The independent variables were normalized to a range from -1 to +1 (Hayes 1974). Quadratic terms of the size parameter and of clipping intensity as well as an interaction term were included in the regression equation (Davies and Goldsmith 1972). A full model, including all possible first and second order terms of the independent variables, was tested. In addition, a regression equation was obtained through a stepwise selection procedure.

The regression equations describe a response surface of shrub productivity in three-dimensional space fitted by the least squares method. Residuals were checked to ensure that the proper model had been used.

4.1.3 Results

Treatment means of current annual growth and leaf biomass are shown in Table 4.1. The initial analysis of variance did not detect significant treatment effects on the production of current annual growth. The significance levels lay between 0.1 and 0.05. It was suspected that the failure to find significant treatment effects was caused by variations of the size of treated plants. A plot of the productivity variables against height and basal diameter demonstrated a statistically significant relationships. The correlation was highest with the basal diameter (Figure 4.1). The inclusion of both height and basal diameter as independent variables into a multiple regression model did not explain a significant amount of additional variation. Consequently, the basal diameter was chosen for the further analysis to adjust for size effects. As the relationships appeared to be linear over the restricted range of basal diameters, no transformation of the data was required.

It was intended to account for size differences of stems with an analysis of covariance. The major assumption of this technique is a homogeneous linear regression coefficient. This assumes that a given increase in size is related to a constant increase in production regardless of the treatment applied. The test of this assumption showed that the analysis of covariance could only be performed for the current annual growth. The F-statistic then showed significant treatment effects (Table 4.2).

The response of current annual growth to different amounts of clipping was expected to be non-linear. The orthogonal partitioning of treatment effects into linear, quadratic, cubic and quartic components was expected to provide clues to the response pattern. Only the quadratic component was significant (Table 4.2). The equation derived from the orthogonal polynomials had a negative coefficient for the quadratic treatment component, indicating that

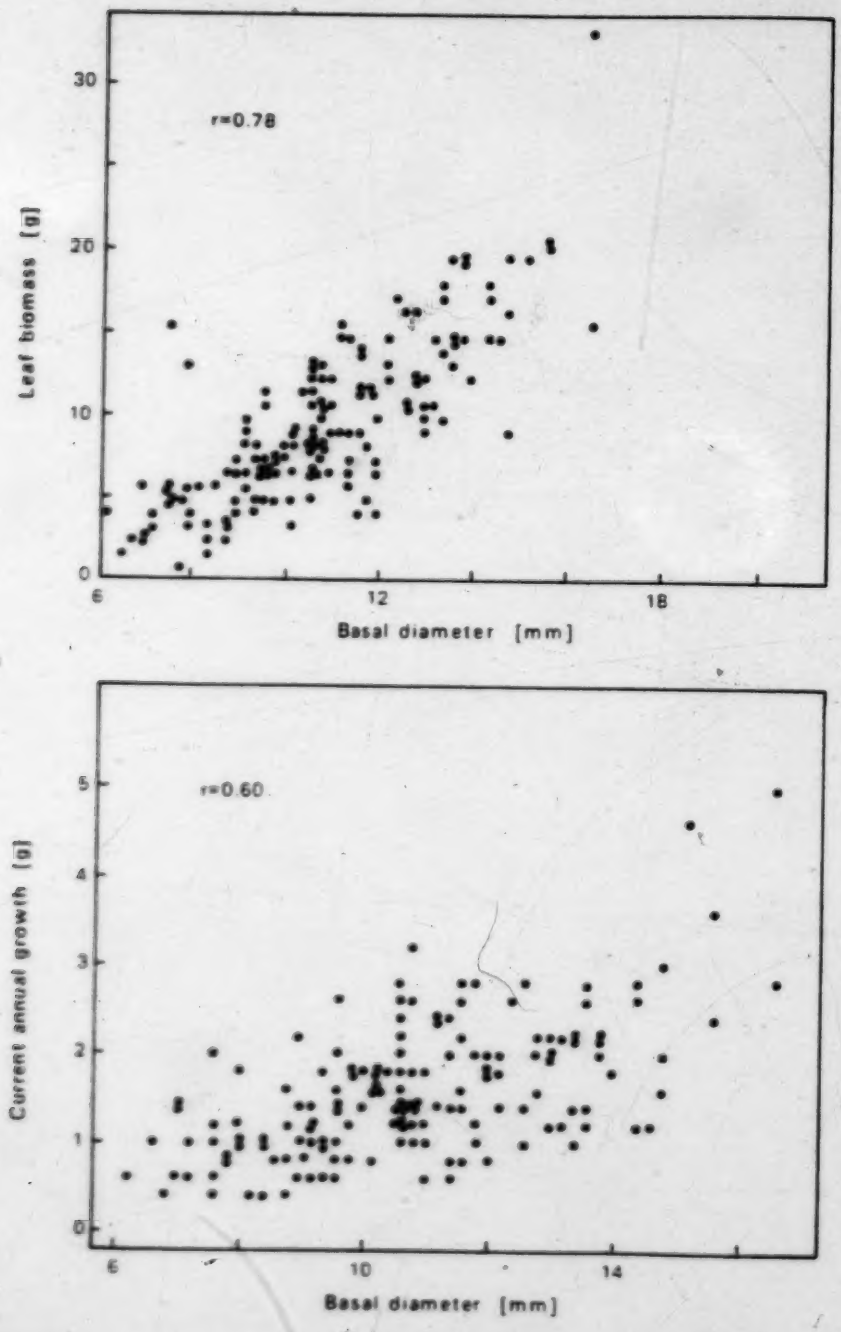

Figure 4.1: The relationship between the productivity of *Corylus cornuta* stems and their basal diameter.

Table 4.1: Mean production of current annual growth (CAG) and leaf biomass (LB) of *Corylus cornuta* stems in relation to five levels of simulated winter browsing. The production of each stem was measured in gram dry-weight. Sample sizes are given in parenthesis.

	CAG						LB					
	Per cent clipping						Per cent clipping					
Block	0	25	50	75	100	Block mean	0	25	50	75	100	Block mean
1	--	1.51 (10)	1.79 (10)	1.34 (10)	1.44 (10)	1.52 (40)	--	8.89 (10)	8.58 (10)	8.22 (10)	9.24 (10)	7.98 (40)
2	--	1.43 (10)	1.75 (10)	1.30 (10)	1.49 (10)	1.49 (40)	--	10.15 (10)	7.24 (10)	7.89 (10)	6.80 (10)	8.02 (40)
3	--	1.63 (10)	1.90 (10)	1.77 (10)	1.23 (10)	1.63 (40)	--	10.50 (10)	13.07 (10)	11.02 (10)	7.58 (10)	10.54 (40)
Treatment means	1.37	1.53	1.82	1.47	1.39	Grand mean 1.51	9.05	9.84	9.63	9.04	6.88	Grand mean 8.89
Standard deviation	0.86	0.57	0.74	0.81	0.54	0.73	5.75	3.65	4.56	5.05	3.51	4.64
Number of samples	(30)	(30)	(30)	(30)	(30)	(150)	(30)	(30)	(30)	(30)	(30)	(150)

Table 4.2: Analysis of covariance table and partitioning of treatment sum of squares of current annual growth for the simulated browsing experiment with *Corylus cornuta*.

ANALYSIS OF COVARIANCE

Source of variation	degrees of freedom	Sum of squares	Mean square	F	significance
Basal diameter (covariate)	1	29.195	29.195	91.577	0.000
Clipping treatment	4	3.390	0.847	2.658	0.035
Residual	144	32.585	0.319		
Total	149	78.492	0.527		

ORTHOGONAL POLYNOMIALS

	Per cent clipping							
	0	25	50	75	100			
Effect*	43.5	44.4	53.7	44.7	40.2	Sum of squares	F	significance
(N)	(30)	(30)	(30)	(30)	(30)			
Coefficients								
Linear	-2	-1	0	1	2	0.132	0.41	n.s.
Quadratic	2	-1	-2	-1	2	2.016	6.32	P<0.025
Cubic	-1	2	0	-2	1	0.051	0.16	n.s.
Quartic	1	-4	6	-4	1	1.167	3.66	n.s.
						3.366 = clipping treatment sum of squares		

*Effects are the totals of adjusted treatment means.

the productivity achieved a maximum. The optimum clipping intensity was found to be near the 50% value.

The homogeneity assumption did not hold for leaf biomass. There appeared to be an interaction between size and treatment effects. As an analysis of covariance was not appropriate, the size of a stem was then considered to be a main factor of interest. The response of leaf biomass and current annual growth to clipping intensity and plant size was determined with a multiple regression analysis. The regression equations (Table 4.3) describe a plane in three-dimensional space which represents the expected response of productivity to any size and clipping combination (Figure 4.2).

Both response surfaces can be described as ascending ridges. Production increased steadily with plant size almost independently of the treatments. This is reflected by the positive regression coefficients for the basal diameter term in the equations. Along the clipping treatment axis the production reached a maximum before it dropped off. The negative regression coefficients of the quadratic treatment term in the equations produce this shape. The maxima are different for the two productivity components. The response surface of current annual growth is almost symmetrical to the mean of the treatment range at 50%. The maximum of leaf biomass production occurred at a much lower clipping intensity (i.e. approximately 25%). It then dropped off very rapidly with higher clipping levels.

4.1.4 Discussion

The purpose of this experiment was to quantify the response of the most frequent shrub species in the forest communities to various degrees of simulated browsing of twigs. The high inherent variability of productivity from stem to stem provided the main problem in the detection of significant effects. Therefore, the experiment was designed to remove much of the variation not related to clipping effects. Additionaly, an attempt was made to keep other factors influencing shrub productivity at a common level.

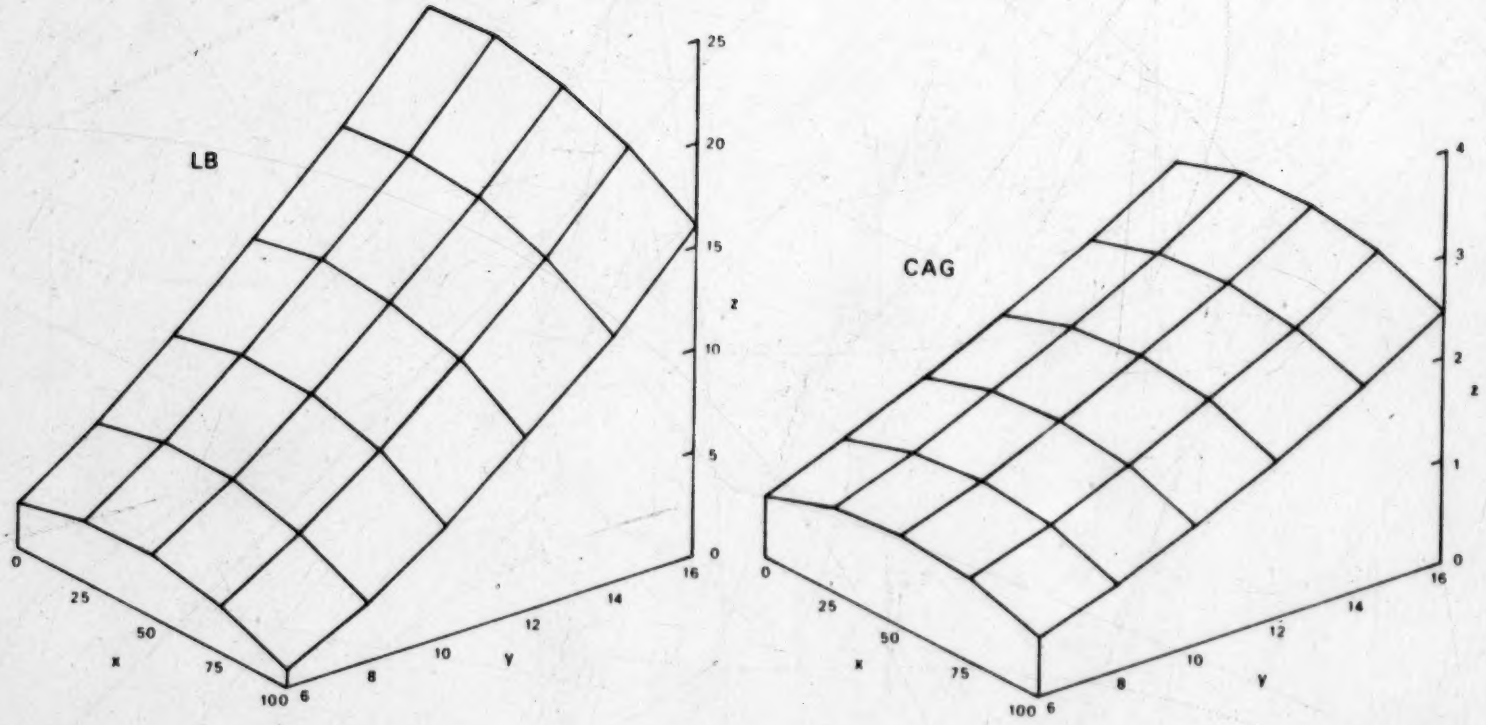

Figure 4.2: Response surfaces of current annual growth (CAG) and leaf biomass (LB; both on z-axis) of *Corylus cornuta* stems in relation to the basal diameter (y-axis; in mm) and the intensity of clipping (x-axis; in per cent). CAG and LB were measured in g dry-weight.

Table 4.3: Polynomial regression analysis of current annual growth (CAG) and leaf biomass (LB) of the simulated browsing experiment with *Corylus cornuta* in Potr-1. The predictor variables per cent clipping (T) and basal diameter (BD) were normalized to a range from +1 to -1.

FULL MODEL	R^2	N	sign.
$LB = -1.3869T + 8.9198BD - 1.6140T^2 + 1.5856BD^2 - 0.6410BDT + 10.6218$	0.72	150	P<0.0001
$CAG = -0.0391T + 1.0451BD - 0.2981T^2 + 0.1841BD^2 - 0.0183BDT + 1.7713$	0.40	150	P<0.0001
STEPWISE SELECTION PROCEDURE			
$LB = 8.6741BD - 1.3587T - 1.4674T^2 + 10.8316$	0.71	150	P<0.0001
$CAG = 1.0064BD - 0.2770T^2 + 1.7933$	0.40	150	P<0.0001

Effects of site quality were minimized by performing the experiment in a single stand. Consequently, the microclimatic conditions were also similar for all experimental units. As the study was restricted to one year, climatic variations from one year to another did not contribute to the variability in the productivity. On the other hand, the long term response pattern emerging from other studies (Aldous 1952, Garrison 1953) could not be determined.

The timing of browsing can also affect the shrub response (Penner 1978, Willard and McKell 1978). During the summer, ungulates feed mainly on green herbage without removing twigs. Many shrubs respond to heavy defoliation with a considerable amount of foliage regrowth during the same summer (Miquelle 1983). Twig removal occurrs mainly in the winter when the plants are dormant. The clipping of dormant plants in late winter was thought to most closely simulate browsing by ungulates.

How well the clipping treatment simulates the natural browsing process is a difficult question to answer. An experiment comparing clipping and grazing of grasses showed a higher productivity for the grazing treatment (Reardon *et al.* 1974). However, Penner (1978) found that responses of willows near Fort Providence, N.W.T., to simulated and natural browsing were very similar. The pattern of natural browsing is somewhat different from the desirably uniform clipping treatments. Haphazard clipping (Krefting *et al.* 1966) or the removal of easily accessible twigs (Penner 1978) may simulate the natural browsing process more realistically. Most twigs of the relatively small *C. cornuta* are easily accessible to browsing ungulates. Still, the animals may consume more than just the current annual growth (Telfer 1976). So it remains difficult to accurately simulate the natural browsing conditions. However, for the statistical analysis of simulated browsing data it is very beneficial to apply the treatments in a uniform way to the experimental units.

Two other factors that control shrub productivity are size and age of a stem. Size parameters are highly correlated with the amount of new growth (section 4.2.3.3). Care had to be taken not to falsely declare treatment effects significant when they were caused by size differences among the treated shrubs. The variation of productivity related to size was partly

reduced by restricting the size of treated plants. Further, the procedures of multiple regression and analysis of covariance were used to adjust for the remaining size variation. The age of stems was not available as an independent variable for this experiment. The correction for age was not essential, because of the weak correlation between age and productivity (Section 3.2.3.3).

The response patterns of other shrub species to clipping are very diverse. For mountain maple (*Acer spicatum*), Krefting *et al.* (1966) found no difference among five clipping intensities. The highest productivity for this species occurred at 100% clipping. White birch (*Betula papyrifera*) increased its productivity with the intensity of the treatment (Aldous 1952). Mountain ash (*Sorbus* sp.) and red-osier dogwood , (*Cornus stolonifera*) were found to produce less twig biomass with increasing clipping intensity (Aldous 1952). For some species the maximum productivity was recorded at intermediate simulated browsing intensities (Willard and McKeel 1978).

The major hypothesis underlying the experiment was that different levels of clipping would affect the productivity of *C. cornuta* stems. Earlier studies had shown a slight to moderate increase in productivity of *C. cornuta* with 25% or 100% of the current annual growth clipped (Aldous 1952). It was expected that the response of *C. cornuta* to clipping might not be linear. With the inclusion of the control shrubs five equally spaced levels of the treatments were available. Hence the data were suited for an analysis of variance and covariance. With the treatment factor being a discrete but quantitative variable, the data were equally well suited for a regression analysis (Draper and Smith 1966).

The analysis of variance was not significant for clipping because productivity was measured on plants with many different sizes. A correction for size was attempted with analysis of covariance. As the assumptions for this procedure were not met for the leaf biomass data, a multiple regression analysis was the proper statistical method to account for size and treatment effects simultaneously. The final regression equations with these two independent variables describe a response surface fitted with the least-squares method. This model can be used to

estimate the production of leaf biomass or current annual growth by previously unbrowsed *C. cornuta* stems at various size and clipping combinations. As such, it is clearly a predictive model. However, the statistical significance of the regression model suggests a definite functional relationship between productivity and simulated browsing intensity.

The shape of the response surface reveals the pattern of productivity related to the two independent variables. The current annual growth response surface (Figure 4.2) resembles a section of an inclined cylinder. The production of current annual growth increases steadily with the basal diameter at any amount of clipping. This implies that there is little interaction between the effects of the two independent variables. The curved plane shows that the maximum of growth can be expected at an intermediate clipping intensity near 50%.

The maximum variation along the treatment axis is small comprising only 12% of the variation along the basal diameter axis. This relationship was also illustrated by the multiple regression coefficients. The regression on basal diameter explained 37% of the variation in the data set. The addition of the quadratic treatment components only accounted for an additional 3% of the total variation. Nevertheless, the highly significant regression demonstrated a definite pattern of twig production in relation to clippping. However,the stimulation of productivity was not as high as for other shrub species (Wolff 1978).

The response surface of leaf biomass depicted slightly different properties (Figure 4.2). The dominant feature was the increase of production with size. Again the variation of productivity in relation to plant size was much greater than the response to clipping. The adjustment for size effects was thus very desirable. The response pattern of leaf biomass differs from the current annual growth at high clipping intensities. Whereas the maximum increase of current annual growth is at the 50% treatment, the maximum amount of leaf production occurred at slightly lower intensities. Thus, the pattern of leaf biomass is not symmetric to the mean clipping intensity of 50%. There was a very sharp drop of leaf production at the 100% treatment. The removal of all buds was largely responsible for this pattern. If several buds are removed, the shrubs may be able to compensate for the loss by increasing leaf growth from the

remaining ones. If many or all buds are removed, new buds have to be initiated at the beginning of the growing season.

One of the implications of the response patterns is the possibility to stimulate the annual forage production of *C. cornuta* through intermediate browsing intensities. However, the increase in twig production is small compared to other shrub species. In the Great Lakes Forest the clipping of willow and mountain maple stimulated their growth to an increase of well over 200% of the original production (Aldous 1952). Considering the comparatively low forage quality rating of *C. cornuta*, not much benefit can be gained from the small increase of productivity at moderate browsing intensities. Larger productivity increments of that species may potentially occur through increased sprouting (Aldous 1952). The resulting higher density may indirectly raise the amount of forage at a site.

The quadratic response pattern to browsing has been found for other shrub species (Garrison 1953). The problem of managing a grazing system to obtain a maximum stimulation of shrub production is frequently related to differences among species in the response to browsing. The optimum grazing intensity varies among shrub species (Aldous 1952). Thus it is impossible to stimulate all species to their maximum production at the same time. Trade-offs between principal and preferred species must be considered (Petrides 1975). At Ministik, the abundance of many of the highly rated forage shrub species like *A. alnifolia, Viburnum edule, C. stolonifera* (USDA 1962) appeared to be limited by browsing. *A. alnifolia* was classified as a decreaser species (Table 3.2). However, it also exhibited numerous signs of browsing in the sanctuary. *C. stolonifera* and *V. edule* only rarely exceeded heights of one meter throughout the study area (e.g. Table 4.6). This demonstrates that both species are severely suppressed. The resistant but less palatable *C. cornuta* was frequently able to achieve heights up to 2.5 m.

The experiment provided evidence for the response in the production of *C. cornuta* to a single clipping treatment. Most simulated browsing studies have involved several years of clipping. Some authors have concluded that sustained treatment can stimulate growth over long periods of time (Aldous 1952, Krefting *et al.* 1966). After clipping was ended, productivity

seemed to decrease again (Davis 1953). The long term effects of browsing on shrub productivity at Ministik could only be studied indirectly. Several different aspects of the response of *A. alnifolia* and *C. cornuta* to the seven years of intensive browsing at Ministik Wildlife Research Station will be discussed in the next section.

4.2 Shrub response to the two grazing systems

4.2.1 Introduction

The question of shrub response to browsing is a very general one. The effects of browsing could be studied on many different levels: on the physiological level of the cells and tissues, on the level of the individual stem or clone, the level of a species or even on the level of the total shrub layer as an integrated physiognomic unit within the plant community. Clearly, different methods and objectives must be involved at each level. The first part of this study had been concentrated on the community level. It revealed changes in the abundance of the different species composing the shrub layer. Estimates of the productivity of the shrub layer in relation to the grazing system were not available through the community survey.

Productivity can be highly variable among plant species due to different intrinsic growth rates and diverse non-linear responses to environmental factors including browsing pressure. Therefore, the study of productivity is more meaningful on the level of a species. As productivity studies can be very laborious, this study was restricted to two shrub species. The focus of this study was again on the most dominant shrub of the aspen forest community: *C. cornuta*. As a counterpart, an important forage species, *A. alnifolia*, was selected. The two species provide an instructive contrast between an increaser and a decreaser species (Table 3.2). The selection of these species resulted in a concentration of research on the aspen forest community. This may be justified by the composition of the shrub layer in this plant community. Gates (1980) observed that in the forest elk fed mainly on *C. cornuta* and *A. alnifolia*, the characteristic shrub species in the aspen forest. Hence, these forest stands are

important as winter foraging sites.

It then became necessary to decide what effects browsing could have on these two species and how to measure them. The intensive browsing within these stands over the seven years of the operation of the MWRS could have severely altered the population dynamics of shrub species. Secondly, the browsing might have changed the growth dynamics (i.e. the production in relation to time or age) of individual stems. Finally, it was attempted to evaluate the productivity of stems and the productivity within a unit area in relation to the grazing intensity. A detailed analysis of age, size and biomass components of shrubs in the two grazing systems was thought to provide clues on all three subjects.

4.2.2 Methods

4.2.2.1 Sampling procedure

Three aspen forest stands (Potr-1, Potr-2, Potr-6) which had already been used for the community survey, were selected for shrub biomass studies of *C. cornuta* and *A. alnifolia* (Figure 2.2). One of them was located in the sanctuary. All shrubs were harvested during the last week of August and the first week of September 1983. At each site at least three $1m^2$ quadrats were placed randomly. All stems of *C. cornuta* and *A. alnifolia* present in the quadrat were clipped at ground level (i.e. the surface of the litter layer). The basal diameter and height of each stem were measured in the field. Additionally, for *C. cornuta* in the stands Potr-6 and Potr-1 two diameters of the crown of each stem were measured at right angles to each other. An estimate of the crown area of each stem was obtained by calculating the area of an ellipse described by the two diameters.

In the lab, all stems were separated into three components: leaves, current annual twig growth and the remaining woody material. All dead material was discarded. The number of missing leaves was recorded. Leaf biomass was adjusted later by adding the missing leaf mass estimated from average leaf weights. No scars of missing twigs were noticed, which showed that the ungulates mainly foraged on green biomass during the

summer. The samples were oven-dried for at least 48 hours. Large stems were dried longer until no more significant moisture loss occurred within a 24 hour period. The dry-weight of the three biomass components was determined for each stem. Total aboveground biomass was calculated by summing the dry weight of the three components. Subsequently, all stems were aged by counting growth rings in the basal section.

The sampling procedure was not well suited to obtaining a large number of stems other than *C. cornuta*. More stems of *A. alnifolia* in the stand were collected on a random walk until the sample comprised approximately twenty shoots of each species. Size restrictions were imposed on *A. alnifolia* stem samples. Only a few stems were harvested with the basal diameter exceeding 2.5 cm since these stems had usually grown well beyond the reach of browsing ungulates.

Additional information on winter forage production was sought for selected shrub species in other community types. A sample of *C. stolonifera* stems was collected in the balsam poplar stand P-1 in the quarter section. The stems of a small and a tall clump of the most common willow *Salix planifolia* were sampled in the narrow willow band of the stand Will-2 in the quarter. Height, basal diameter and biomass measurements were made on the stems of these species.

4.2.2.2 Statistical analysis

For each stem of these four shrub species, six parameters were derived. In addition, the measurements pertaining to *C. cornuta* were based on unit area samples. The initial statistical analysis of these data was concentrated on *C. cornuta*. Relative frequency distributions were calculated for each parameter. The univariate distribution of size measurements and ages were called size and age structure. The histograms were compared among sites.

Next, scatterdiagrams of size and biomass parameters plotted against age were examined. As measurements had been taken at a single point in time, patterns of the size and biomass attributes in relation to age were thought to provide some information on the

growth dynamics of these shrubs with respect to different grazing regimes.

A common approach to estimate biomass of plants is to establish a statistical relationship between dimensions of a shoot and the weight of the shoot or some of its components (Murray and Jacobsen 1982). Often these relationships are non-linear (Brown 1976). The natural logarithms of all six variables were calculated. Scatter diagrams were used to check whether the resulting relationship tended to be linear. Least-squares regressions were computed to predict biomass (i.e. leaf biomass, current annual growth and total aboveground biomass) from the size of a stem. If the correlation between biomass and height or basal diameter was not high, a stepwise multiple regression analysis was performed to predict the biomass with the aid of several parameters.

The logarithmic transformation had the further effect of making the variance of a variable independent of its magnitude. This allowed a statistical evaluation of the regression coefficients of different sites. First, a test for the homogeneity of the regression coefficients of all three sites was carried out according to Steel and Torrie (1980). The results were compared with t-tests of the difference of the slopes of the regression line between pairs of sites. Similar regressions of logarithmically transformed data were computed for *A. alnifolia*, red-osier dogwood and the willow species.

A second approach to measure shrub biomass in relation to the grazing system was taken for *C. cornuta*. The totals of basal area, leaf biomass, current annual growth and total aboveground biomass of this species was calculated for each sample quadrat. A one-way analysis of variance was used to evaluate differences among the three stands. The difference of stand means was tested with the Tukey's *w* procedure for multiple comparisons (Steel and Torrie 1980). The biomass totals for each quadrat were plotted against basal area and density on double logarithmic paper. Basal area and density were used as concomitant variables in an analysis of covariance of the biomass variables. The difference of adjusted stand means was tested as described by Steel and Torrie (1980).

4.2.3 Results

4.2.3.1 Frequency distributions

The pattern of relative frequencies of age or size of stems is termed its age and size structure. The two main size parameters of shrubs were height and basal diameter. The relative frequencies of height and diameter classes of *C. cornuta* in three aspen forest stands are depicted in Figures 4.3 and 4.4. The height distributions in the two stands in the quarter section seem to be cut off at around 150 cm, whereas stems up to 250 cm were recorded in the sanctuary. The mean of height and basal diameter of *C. cornuta* in Potr-2 was lower than in the other stands. The shape of the basal diameter distribution was different among the three stands. The size structure of *C. cornuta* was considerably skewed in the stands Potr-1 and Potr-6. The distributions were skewed to the right in the sanctuary and to the left in the quarter section.

The histograms of the approximate crown area of *C. cornuta* stems best illustrate morphological differences due to browsing impact (Figure 4.5). In the heavily browsed aspen forest-stand Potr-6, the crowns were small and uniform. In the sanctuary, a much wider range of crown areas was recorded with a greater mean.

The age structures of these stems in the same stands are shown in Figure 4.6. The *C. cornuta* stems in the two stands of the quarter section appear to have a bimodal distribution. The modes have approximately the same height. The peaks of the two stands do not coincide. The age structure of the stand in the sanctuary also shows a slight bimodality. However, the variability among age classes is very high. The two stands of the quarter section (Potr-2 and Potr-6) were pooled to increase the sample size. The cumulative age distributions then presented a clearer picture (Figure 4.7). These distributions decrease in an almost linear fashion. This means that the numbers of stems in each age class remain roughly the same for the first ten years.

The small sample size and the stem size restrictions of the sampling procedure hinder the interpretation of age and size structure diagrams of *A. alnifolia*. Little

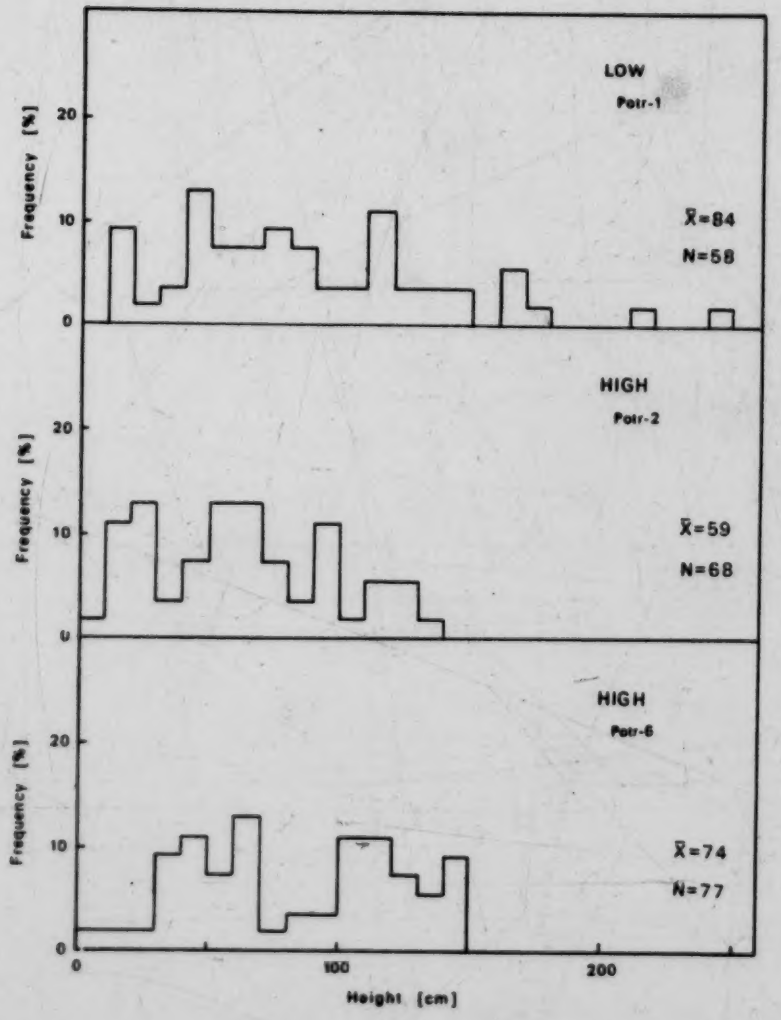

Figure 4.3: Relative frequency of heights of *Corylus cornuta* stems in relation to low and high browsing pressure.

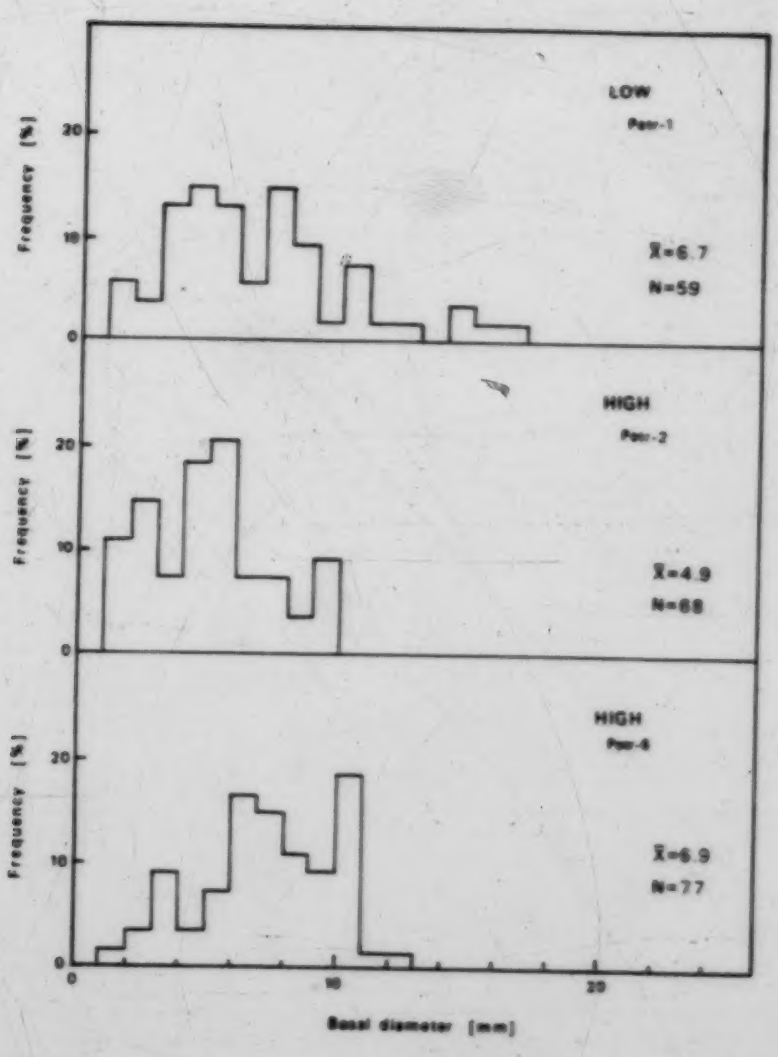

Figure 4.4: Relative frequency of basal diameters of *Corylus cornuta* stems in three aspen forest stands in relation to low and high browsing pressures.

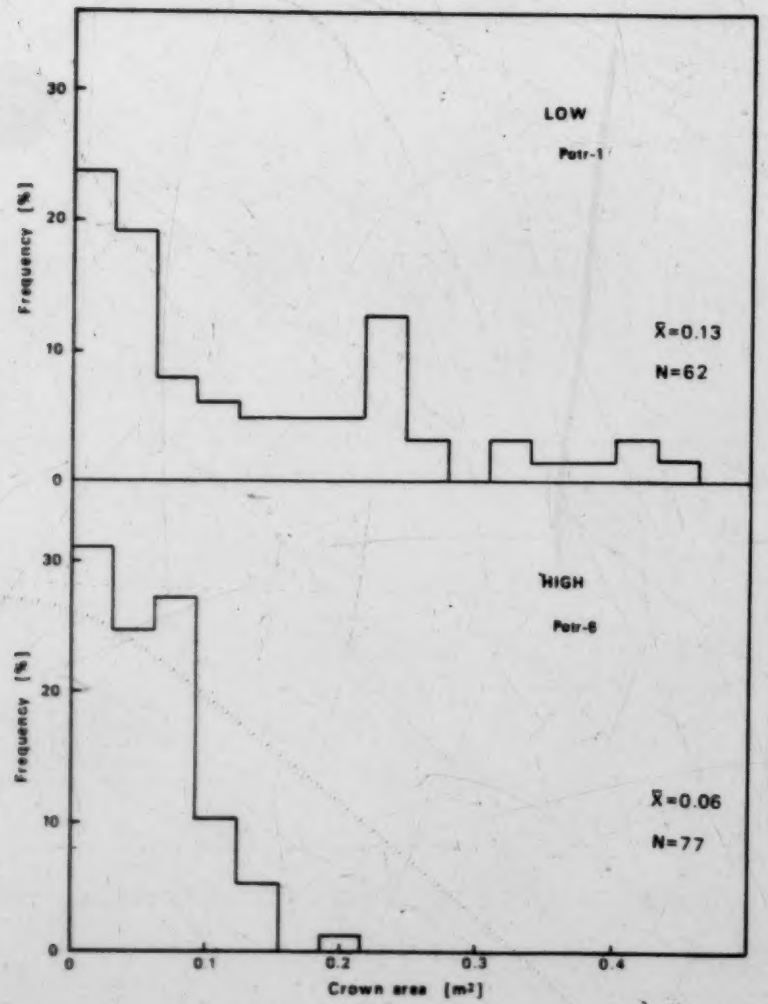

Figure 4.5: Relative frequency of approximate crown areas of *Corylus cornuta* stems in two aspen forest stands in relation to low and high browsing pressures.

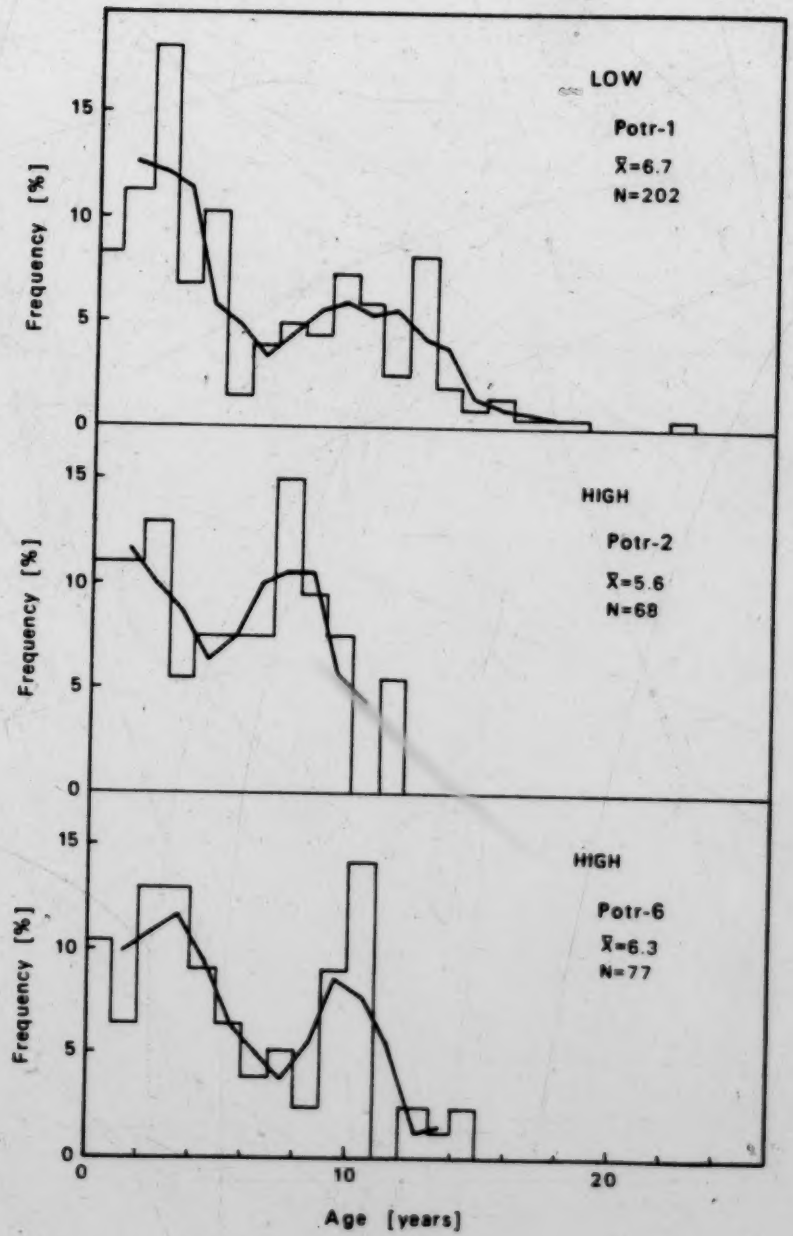

Figure 4.6: Age structure with three year moving average of *Corylus cornuta* stems in three aspen forest stands in relation to low and high browsing pressures.

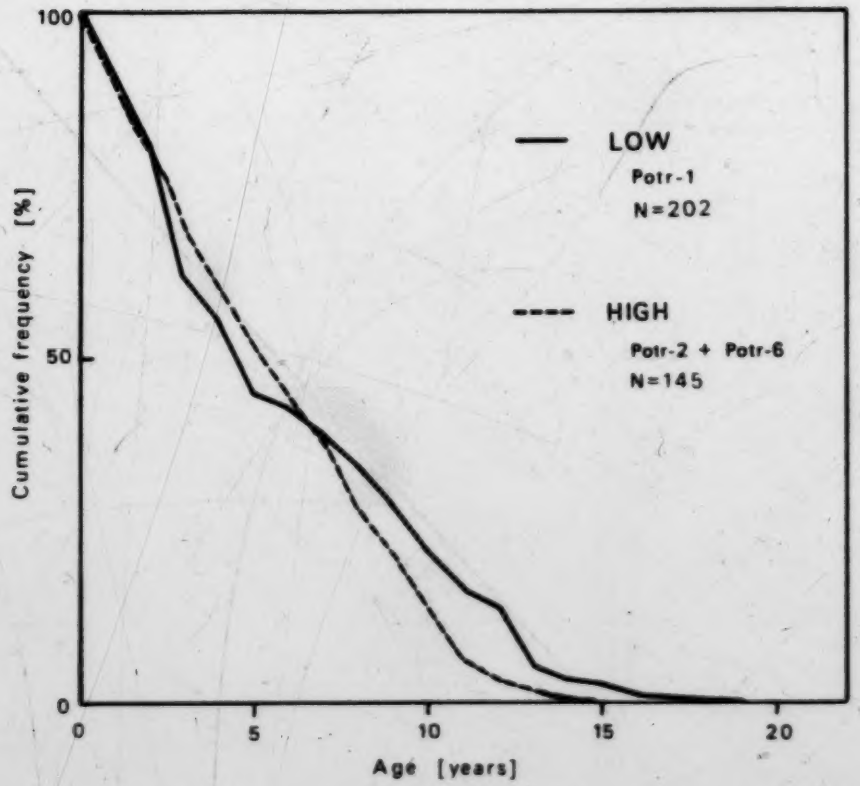

Figure 4.7: Cumulative age distribution of *Corylus cornuta* stems in the aspen forest in relation to low and high browsing intensities.

informative value was found in the frequency distributions (Figure 4.8). However, it was interesting to see that the range of stem ages for this species was much larger than for *C. cornuta*. The oldest stems of *A. alnifolia* in the stand Potr-1 may date back to the stand origin.

For the purpose of a comparison of the productivity and biomass of individual shoots, the frequency distributions of leaf biomass, current annual growth and total aboveground biomass in the three stands are shown in Figure 4.9. The distributions of all three variables are strongly skewed to the right. In all three stands, shoots with low amounts of leaf biomass and current annual growth and a low total aboveground biomass are more frequent than shoots with large biomass values. The frequency distributions depict larger values in the aspen forest stand of the sanctuary. The frequency distributions for the stands in the quarter section are cut off at lower values. The shoots of *C. cornuta* in the stand Potr-2 seem to have lower values than in the other two stands. This pattern is also illustrated by a much greater proportion of shoots with leaf biomass, current annual growth, total aboveground biomass, basal diameter and height below the median of all sampled stems.

4.2.3.2 Age relationships

For each stand the variables describing size and biomass of the *C. cornuta* stems were plotted against age (Figures 4.10 and 4.11). The diagrams were expected to reveal some age dependencies of these parameters. The basal diameter, height and shoot area were positively correlated to the age of the stem. All correlations were significant, but the amount of variation explained by the age relationship was generally low ($0.29 < R^2 < 0.60$). The ranges of the size parameters in the stands of the quarter section were smaller with considerably lower maximum values.

In contrast to the other variables, stem age is a discrete variable. The mean values in each age group were calculated and plotted on the graph to clarify general trends. Curvilinear relationships were expected, but they were not clear from the diagrams. Few

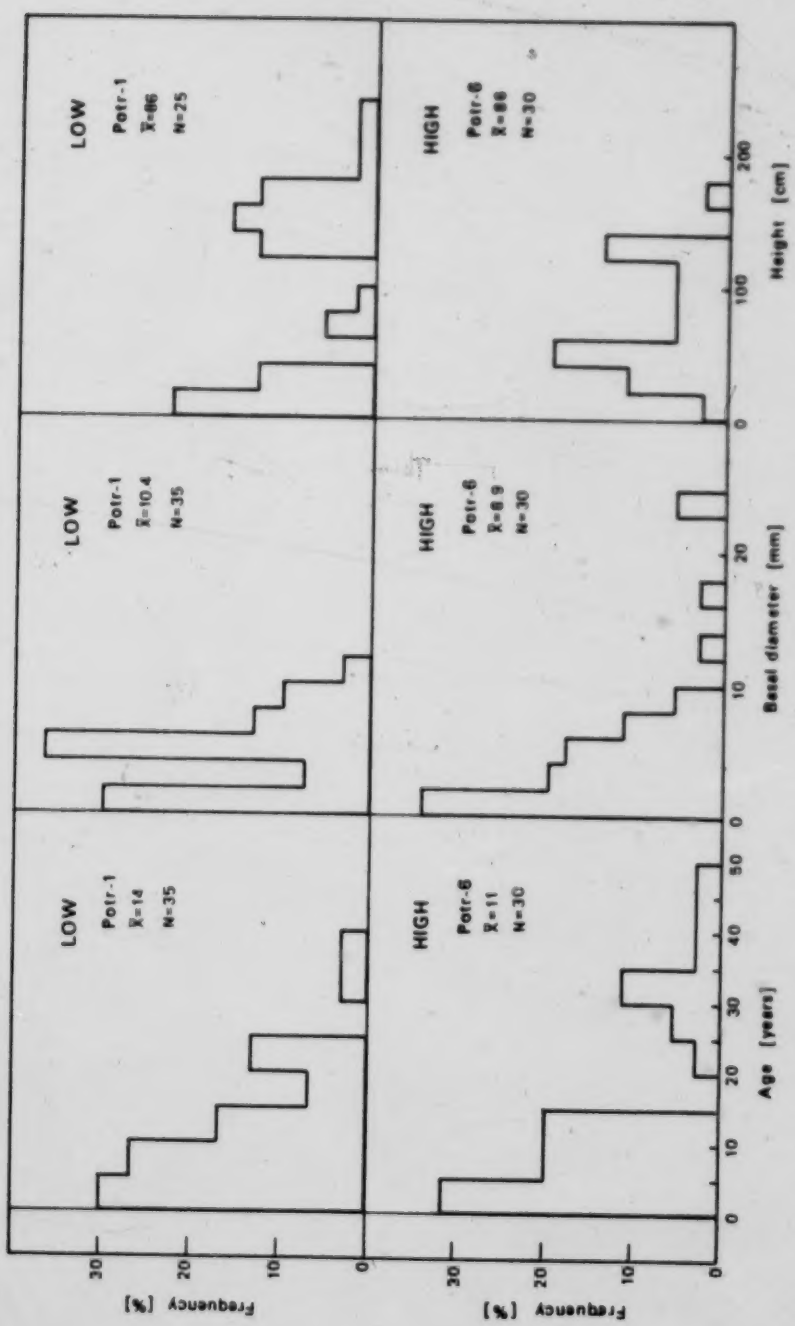

Figure 4.8: Age and size structure of *Amelanchier alnifolia* in two aspen forest stands in relation to low and high browsing pressure.

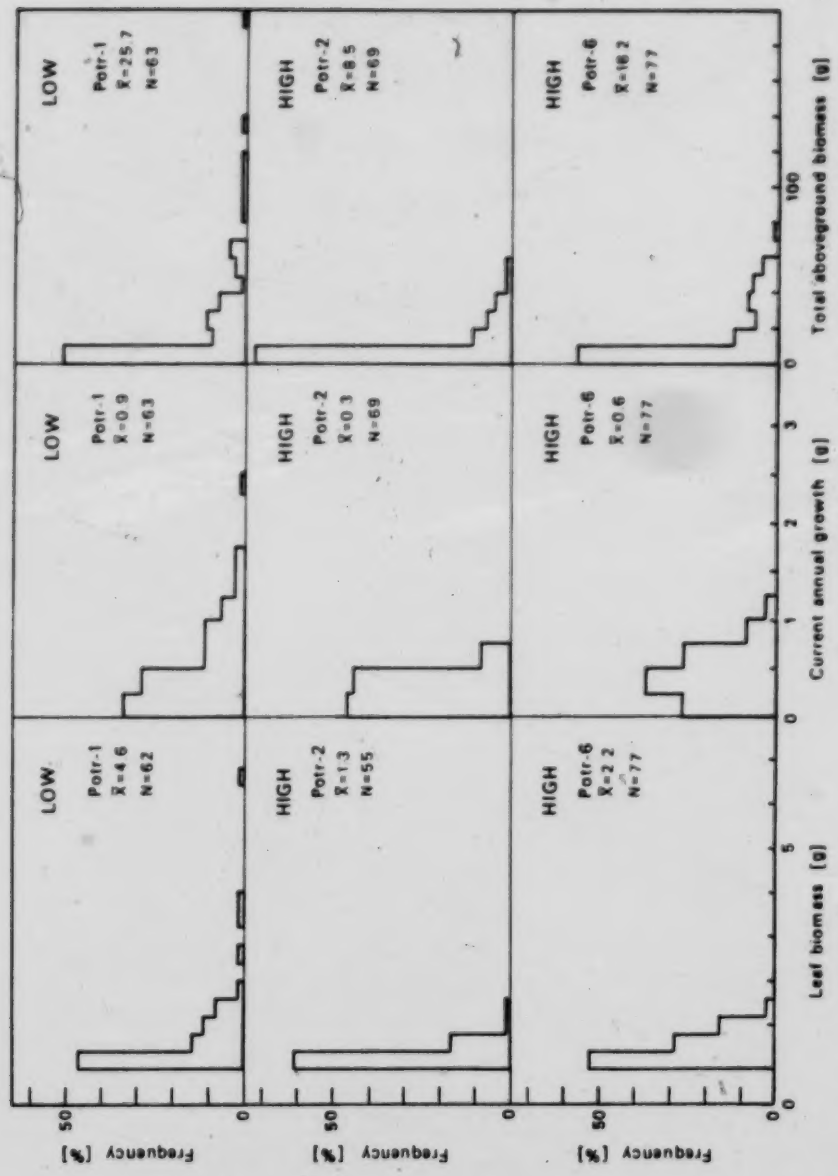

Figure 4.9: Relative frequency of shrub biomass of *Corylus cornuta* in three aspen forest stands in relation to low and high browsing pressure.

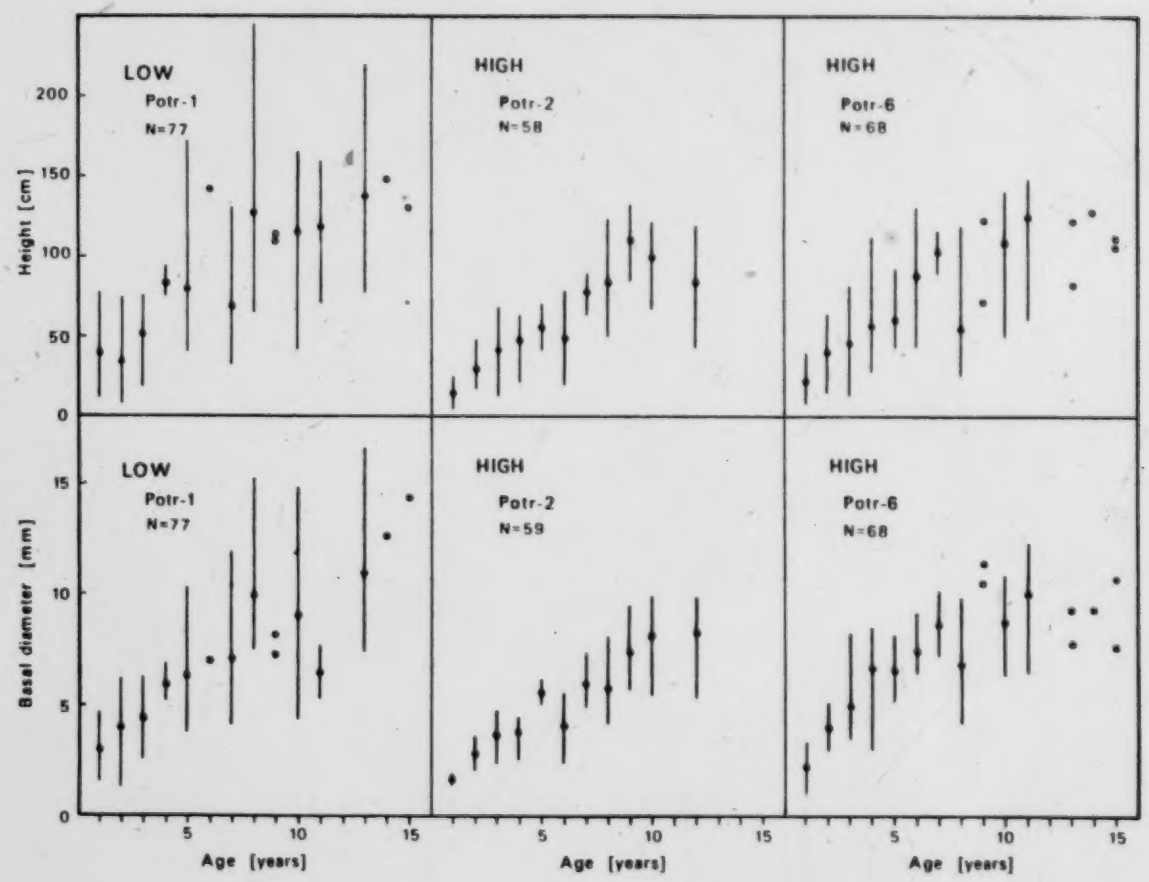

Figure 4.10: Means and standard deviations of the size of *Corylus cornuta* stems in relation to their age in stands with low and high grazing intensities.

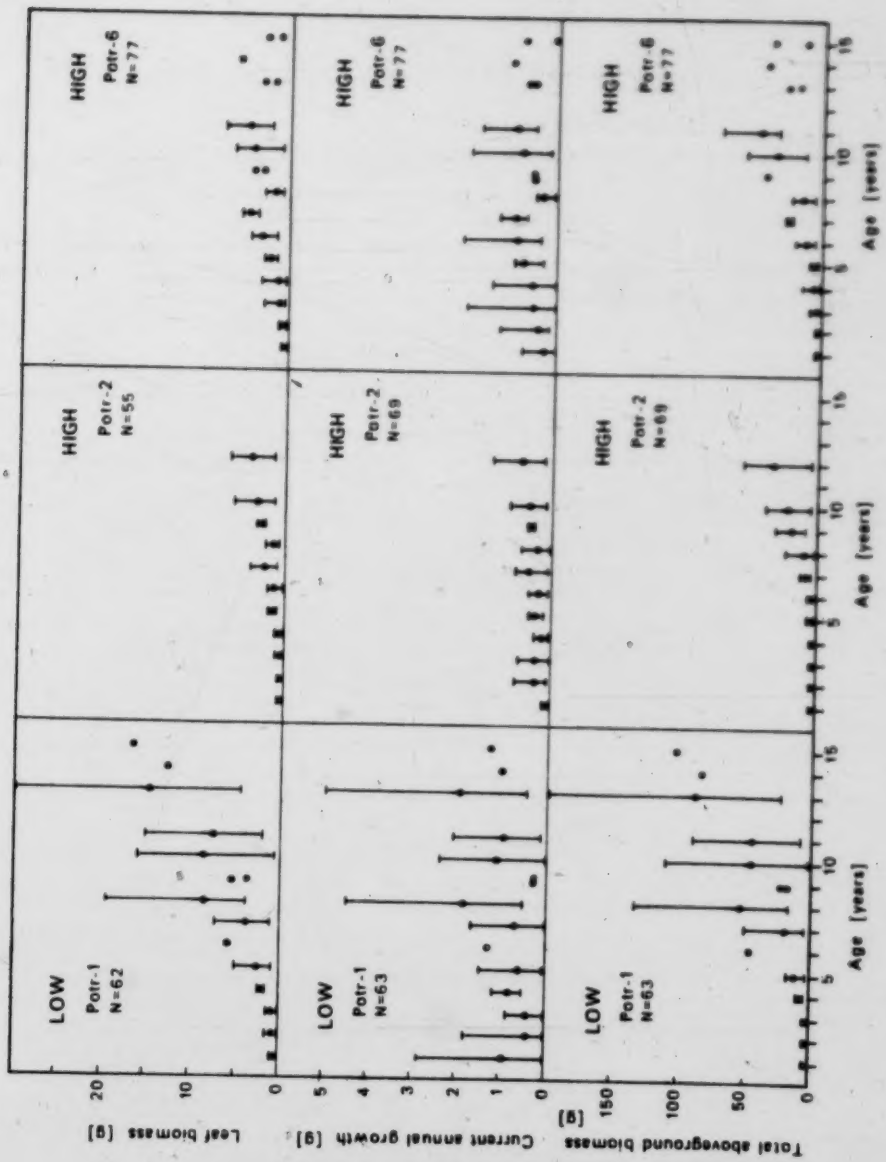

Figure 4.11: Means and standard deviations of the biomass of *Corylus cornuta* stems in relation to their age in stands with low and high grazing intensities.

samples of old stems and the increasing variability of size with age, further helped to obscure any underlying patterns.

The plots of leaf biomass and total aboveground biomass *versus* age were similar to the above. They displayed a fan-shaped pattern indicating the increase in variance with age. The variability of stems sampled in the quarter section was again much lower, because the upper ranges of biomass were much reduced. The abscissa formed the lower limit for leaf biomass and total aboveground biomass. The poorest relationship was found for the current annual growth. Its correlation to age is significant only for the stand Potr-2, where it accounted for 16% of the variation only. The relationships of the age of *A. alnifolia* stems to its biomass component were poor (Figure 4.12). No differences were found between stems in the different grazing systems, because the variability among stems was very high.

4.2.3.3 Regression analysis

Size parameters are commonly used to estimate biomass and productivity of plants. Height and basal diameter are some of the most widely used dimensions to predict the mass of a shoot or of its parts. Scatter diagrams of logarithmically transformed data showed a high degree of linear correlation between the size (height, basal diameter) and the leaf biomass and total aboveground biomass of the *C. cornuta* stems (Figures 4.13 and 4.14). The regression equations are shown in Table 4.4. The relationship between current annual growth and size parameters was highly significant but much less variation could be explained by the regression (Figure 4.15).

The next step was to compare the regression equations among the three stands. A test for the homogeneity of the regression coefficients (Steel and Torrie 1980) showed that only the slopes of the regression lines for total aboveground biomass were not significantly different in the three stands (Table 4.4). The regression coefficients were then compared among individual stands (Figure 4.16). No significant differences were found between the regressions in the stands Potr-6 and Potr-2 both located in the quarter section. Regression

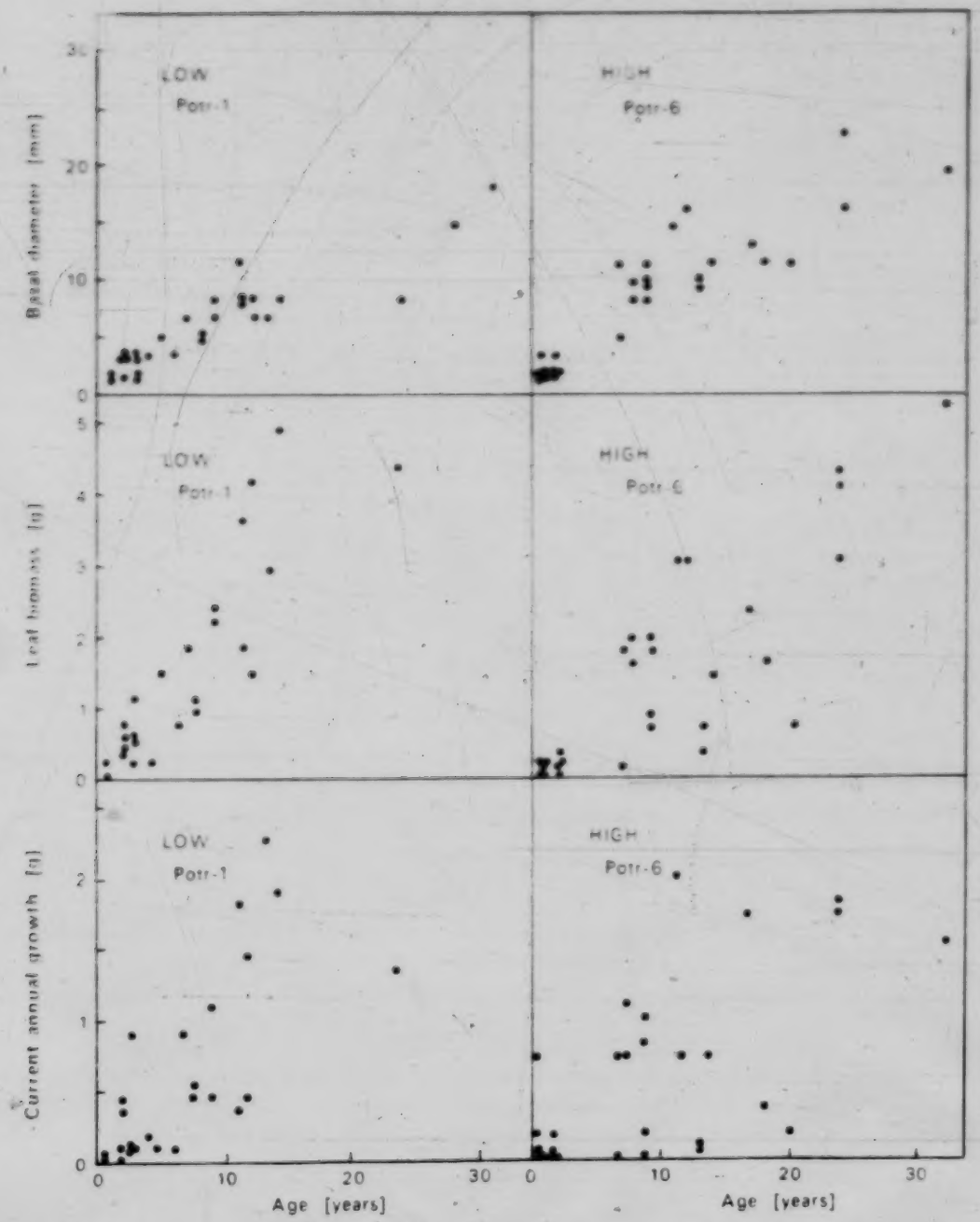

Figure 4.12: Size and production of stems of *Amelanchier alnifolia* in relation to their age in stands with low and high grazing intensities.

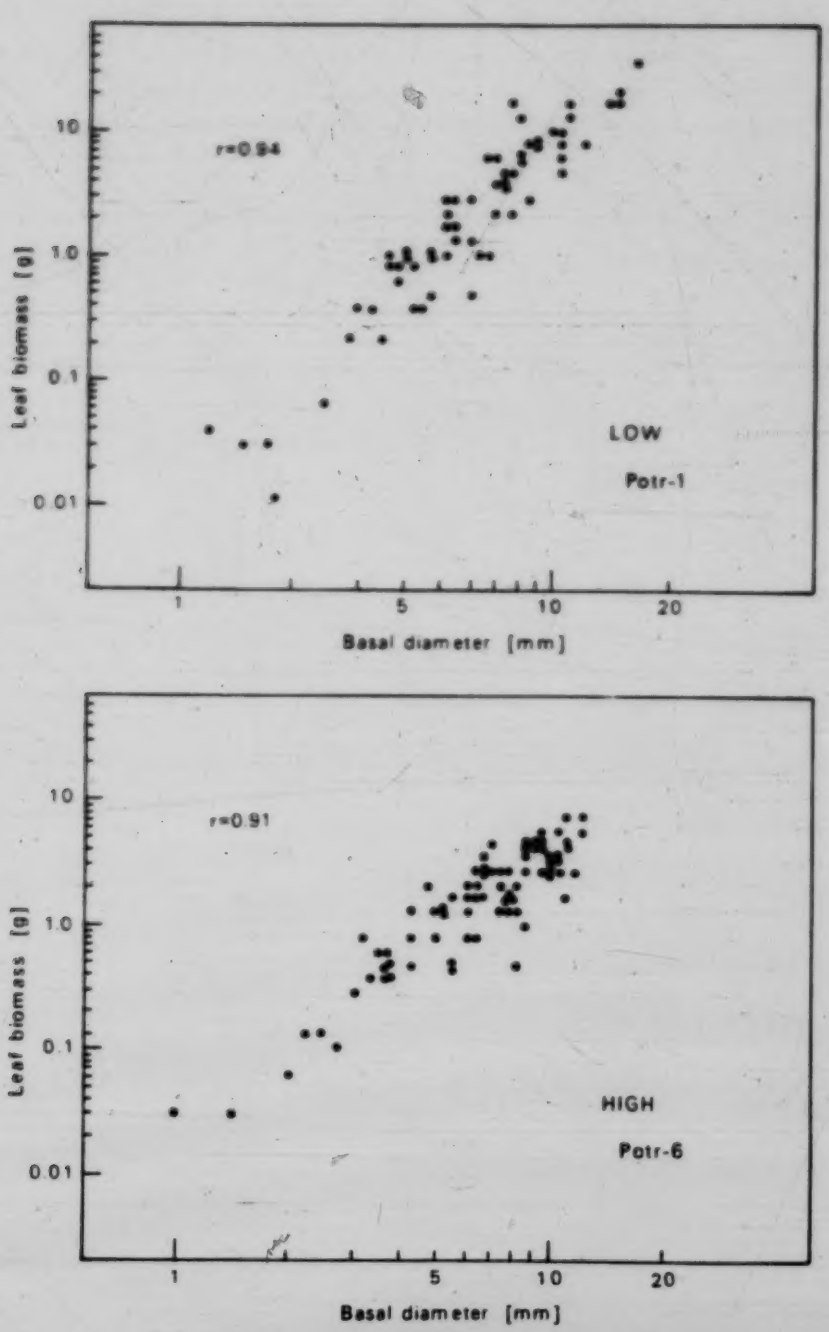

Figure 4.13: Relationship between basal diameter and leaf biomass of *Corylus cornuta* stems in stands with low and high grazing intensities.

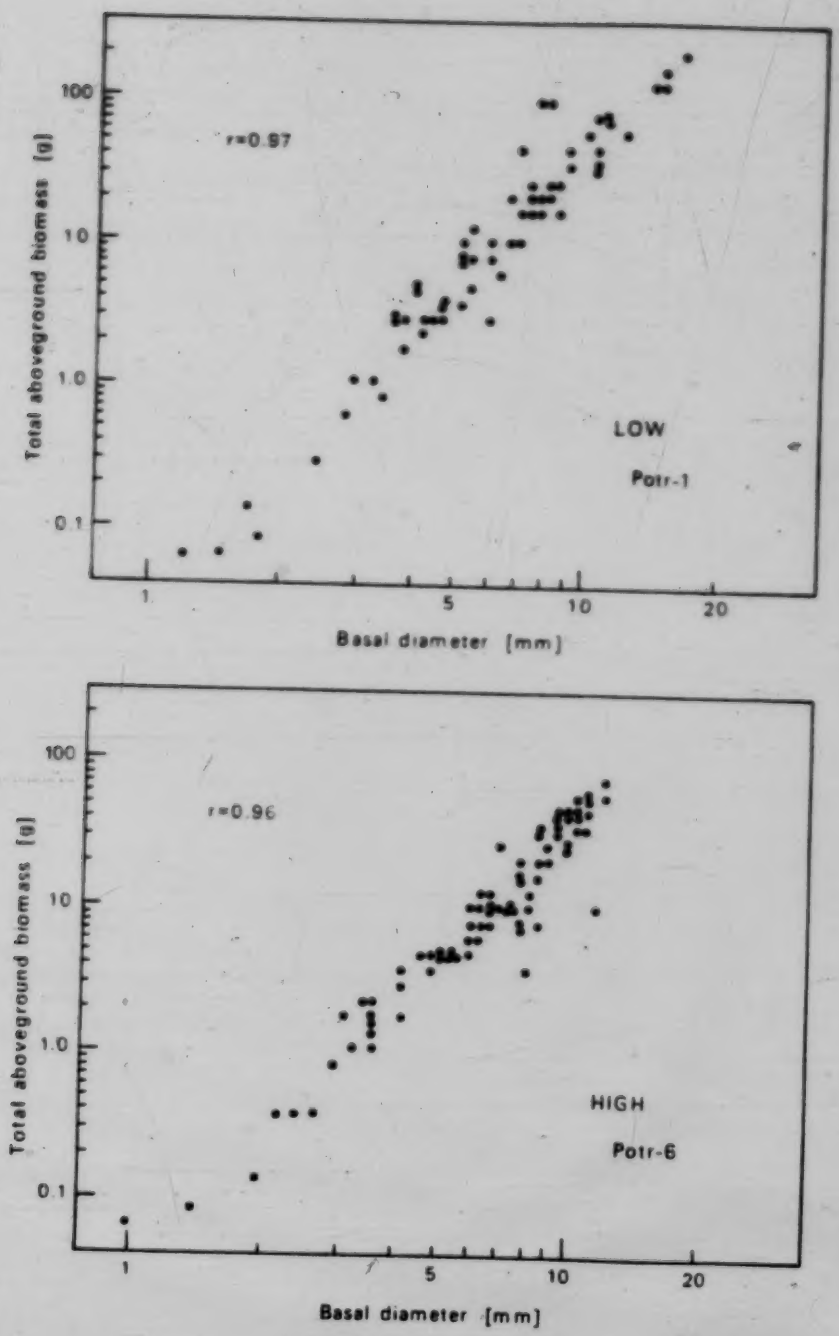

Figure 4.14: Relationship between basal diameter and total aboveground biomass of *Corylus cornuta* stems in stands with low and high grazing intensities.

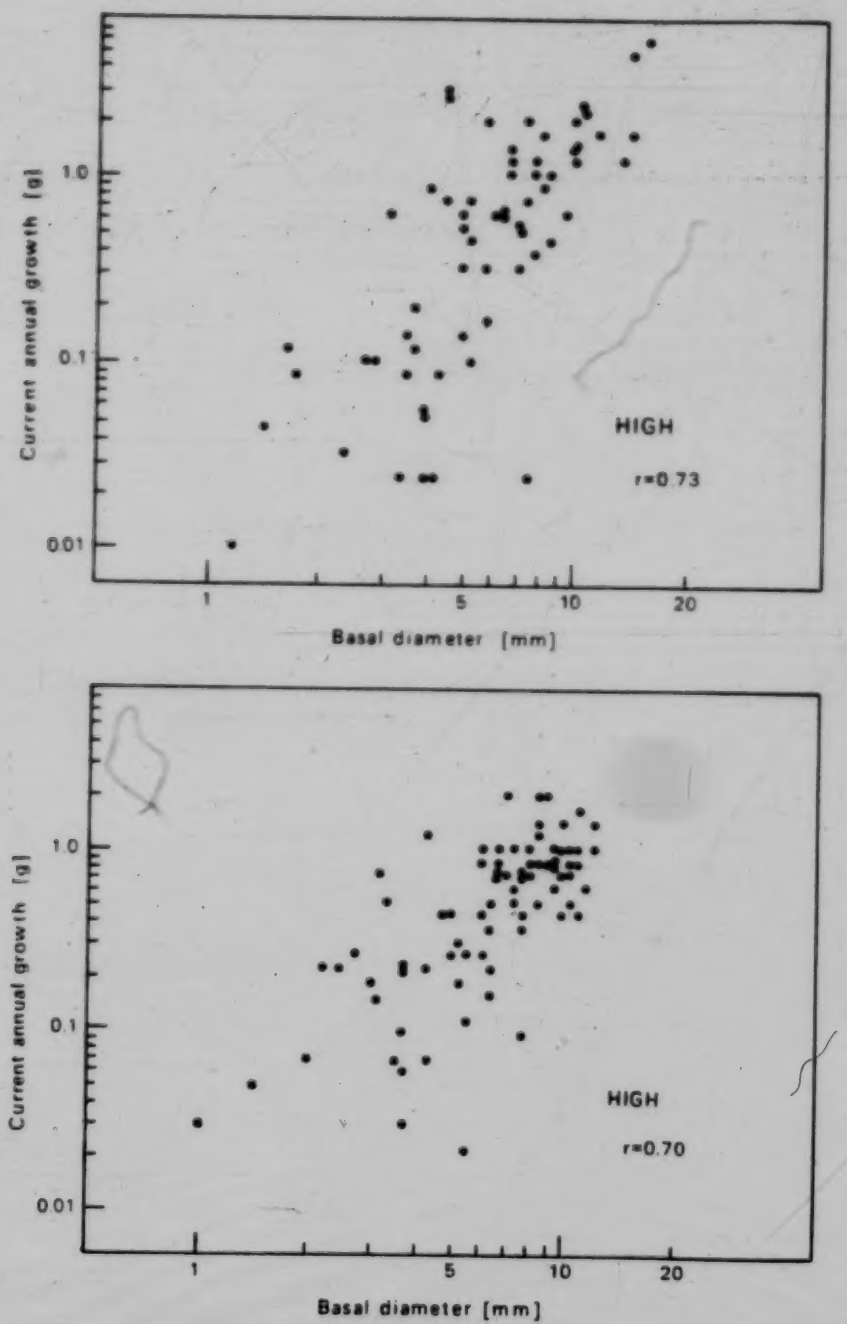

Figure 4.15: Relationship between basal diameter and current annual growth of *Corylus cornuta* stems in stands with low and high grazing intensities.

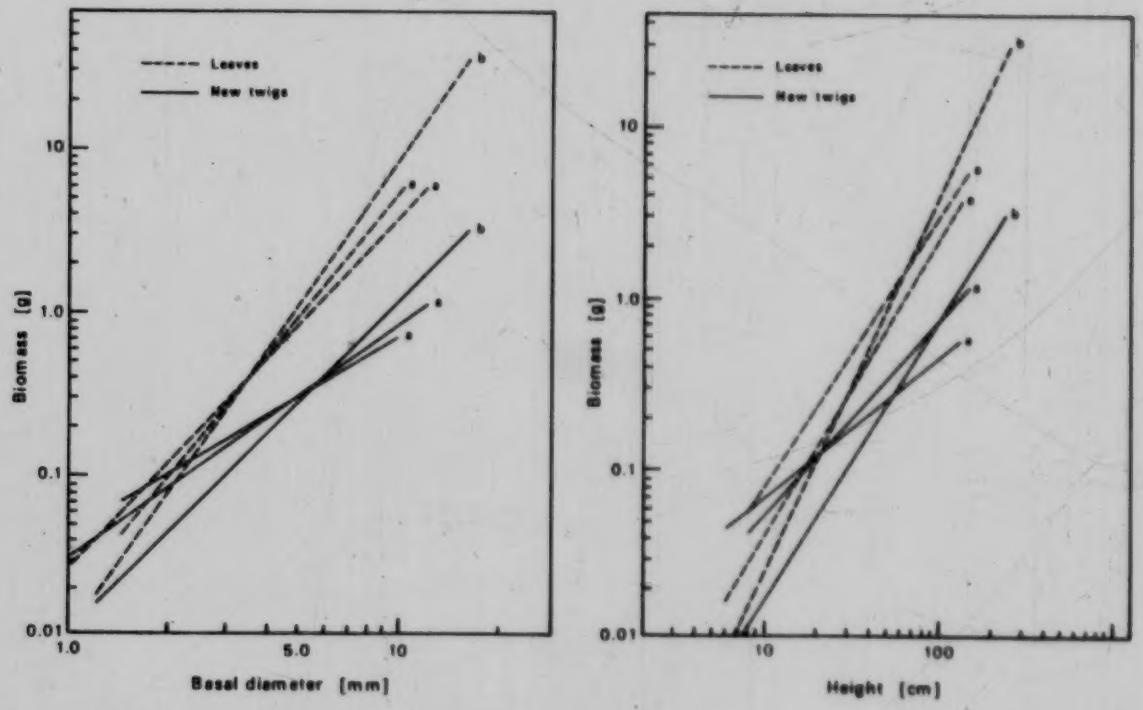

Figure 4.16: Comparison of regression lines for *Corylus cornuta* among three aspen forest stands. The slopes of lines with the same letters are not significantly different at the 0.05 probability level. Lines denoted with a and b are from stands with high and low browsing intensity respectively.

Table 4.4: Coefficients of linear regression analysis of logarithmically transformed biomass (LB=leaf biomass, CAG=current annual growth, TB=total aboveground biomass) and size parameters (HT=height, BD=basal diameter) of stems of *Corylus cornuta* in three aspen forest stands.

	BIRD SANCTUARY Potr-1			QUARTER SECTION OF MWRS Potr-2			Potr-8			test for homogeneity
	a (SE)	*b* (SE)	R^2 (N)	*a* (SE)	*b* (SE)	R^2 (N)	*a* (SE)	*b* (SE)	R^2 (N)	(of *b*'s)
Regression equation										
ln(LB)=*a*+*b*ln(HT)	-8.5791 (0.491)	2.1576 (0.115)	0.86 (77)	-7.1228 (0.401)	1.7163 (0.101)	0.85 (54)	-6.1030 (0.385)	1.5660 (0.385)	0.78 (60)	not homog. P<0.005
ln(CAG)=*a*+*b*ln(HT)	-7.7860 (0.736)	1.6219 (0.172)	0.61 (77)	-4.5155 (0.482)	0.8131 (0.121)	0.46 (54)	-5.4013 (0.503)	1.1073 (0.121)	0.53 (60)	not homog. P<0.005
ln(TB)=*a*+*b*ln(HT)	-8.3002 (0.424)	2.4509 (0.099)	0.91 (77)	-7.5311 (0.359)	2.2257 (0.090)	0.92 (54)	-6.8567 (0.408)	2.1509 (0.098)	0.87 (60)	homog.
ln(LB)=*a*+*b*ln(BD)	-4.5523 (0.246)	2.8883 (0.132)	0.89 (77)	-3.9912 (0.178)	2.4385 (0.113)	0.90 (54)	-3.5693 (0.213)	2.1339 (0.112)	0.83 (60)	not homog. P<0.005
ln(CAG)=*a*+*b*ln(BD)	-4.4684 (0.444)	2.0025 (0.239)	0.54 (77)	-3.0660 (0.250)	1.1783 (0.160)	0.51 (54)	-3.4572 (0.317)	1.4254 (0.167)	0.49 (60)	not homog. P<0.005
ln(TB)=*a*+*b*ln(BD)	-3.7015 (0.204)	3.2653 (0.110)	0.94 (77)	-3.4348 (0.136)	3.1383 (0.087)	0.96 (54)	-3.4392 (0.184)	2.9649 (0.971)	0.93 (60)	homog.
Range of predictor variables	min.	max.		min.	max.		min.	max.		
HT [in cm]	7.0	245.0		6.0	133.0		8.0	148.0		
ln(HT)	1.946	5.501		1.792	4.890		2.079	4.997		
BD [in mm]	1.2	16.6		1.4	9.9		1.0	12.3		
ln(BD)	0.182	2.809		0.336	2.293		0.000	2.510		

coefficients for leaf biomass and current annual growth were significantly different between the stand in the sanctuary and both stands in the quarter. The regressions on total aboveground biomass were different only for the stands Potr-6 and Potr-1. In all cases the slope of the linear regression line was greater in the lightly browsed stand Potr-1. This implies that for a given size increment a larger production increment can be expected in this stand. The difference in slope also implies that the regression lines intersect each other (Figure 4.16). The leaf biomass and current annual growth in the quarter is larger below the points of intersection with the line of stand Potr-1. Above these points the biomass was lower.

The simple linear regressions of biomass on size were also highly significant for *A. alnifolia* (Table 4.5). Again, the current annual growth was much more scattered around the regression line. In contrast to *C. cornuta*, the regression coefficients were not different between the two sites. Consequently, it was justified to calculate a pooled regression for this species. Regression coefficients were also obtained for two shrub species (Table 4.6) sampled in the quarter section only, *Salix planifolia* and *C. stolonifera*.

The correlation between current annual growth and size of all shrubs was lower than the one for leaf biomass and total aboveground biomass. An attempt was made to improve the regression on current annual growth by an inclusion of further independent variables. Two sets of predictor variables were offered to the regression program. The first set included the logarithms of height, basal diameter, age and leaf biomass. The second contained the same variables except for leaf biomass.

The stepwise multiple regression analysis showed that 15-20% of the variation of current annual growth could be explained by the addition of two or three variables to the regression equation (Table 4.7). In the first step, the program selected the variable with the highest correlation. This first predictor variable was different among the sites. In the stand Potr-6 leaf biomass was the first variable included in the equation. If leaf biomass was not offered in the independent variable list, height was selected in the first step for this

Table 4.5: Coefficients of linear regression analysis of logarithmically transformed biomass (LB=leaf biomass, CAG=current annual growth, TB=total aboveground biomass) on size parameters (HT=height, BD=basal diameter) of stems of *Amelanchier alnifolia* in two aspen forest stands.

	BIRD SANCTUARY Potr-1			QUARTER SECTION OF MWRS Potr-2			POOLED REGRESSION		
	a (SE)	*b* (SE)	R^2 (N)	*a* (SE)	*b* (SE)	R^2 (N)	*a* (SE)	*b* (SE)	R^2 (N)
Regression equation									
ln(LB)=*a*+*b*ln(HT)	-6.4684 (0.583)	1.5219 (0.136)	0.85 (25)	-5.6583 (0.397)	1.2842 (0.094)	0.88 (28)	-5.8852 (0.330)	1.3609 (0.078)	0.86 (53)
ln(CAG)=*a*+*b*ln(HT)	-7.8084 (1.271)	1.5845 (0.296)	0.56 (25)	-5.6738 (0.629)	1.1099 (0.149)	0.68 (28)	-6.2812 (0.608)	1.2416 (0.143)	0.60 (53)
ln(TB)=*a*+*b*ln(HT)	-8.5640 (0.524)	2.4352 (0.122)	0.95 (25)	-7.5307 (0.425)	2.3830 (0.100)	0.96 (28)	-7.8359 (0.417)	2.3643 (0.098)	0.92 (53)
ln(LB)=*a*+*b*ln(BD)	-2.5468 (0.270)	1.7490 (0.173)	0.82 (25)	-3.3575 (0.269)	1.5474 (0.129)	0.85 (28)	-2.5712 (0.254)	1.3896 (0.136)	0.67 (53)
ln(CAG)=*a*+*b*ln(BD)	-3.9499 (0.492)	1.9765 (0.315)	0.63 (25)	-3.5575 (0.432)	1.5474 (0.206)	0.59 (28)	-3.3909 (0.333)	1.3465 (0.178)	0.53 (53)
ln(TB)=*a*+*b*ln(BD)	-2.3686 (0.214)	2.6540 (0.137)	0.95 (25)	-3.4087 (0.199)	2.9485 (0.095)	0.97 (28)	-2.6396 (0.196)	2.7458 (0.105)	0.93 (53)
Range of predictor variables	min.	max.		min.	max.				
HT [in cm]	7.0	212.0		10.0	292.0				
ln(HT)	1.95	5.36		2.30	5.68				
BD [in mm]	1.4	22.1		1.1	8.9				
ln(BD)	0.34	3.10		0.10	2.19				

Table 4.6: Coefficients of regression analysis of biomass components on size parameters of *Salix planifolia* and *Cornus stolonifera* in the quarter section.

Equation	*Salix planifolia* a (SE)	b (SE)	R^2 (N)	*Cornus stolonifera* a (SE)	b (SE)	R^2 (N)
$\ln(LB)=a+b\ln(HT)$	-4.0117	1.1215	0.54	-7.7152	1.9896	0.76
	(0.764)	(0.170)	(40)	(0.969)	(0.245)	(23)
$\ln(CAG)=a+b\ln(HT)$	-6.1906	1.4110	0.42	-9.3451	1.9433	0.54
	(1.212)	(0.269)	(40)	(1.563)	(0.396)	(23)
$\ln(TB)=a+b\ln(HT)$	-1.8871	1.1677	0.62	-8.1175	2.4502	0.91
	(0.670)	(0.149)	(40)	(0.674)	(0.171)	(23)
$\ln(LB)=a+b\ln(BD)$	-6.2648	3.1262	0.57	-2.9156	1.9180	0.54
	(0.890)	(0.381)	(40)	(0.619)	(0.383)	(23)
$\ln(CAG)=a+b\ln(BD)$	-9.5942	4.1786	0.56	-4.2476	1.6130	0.29
	(1.386)	(0.594)	(40)	(0.902)	(0.558)	(23)
$\ln(TB)=a+b\ln(BD)$	-4.3601	3.3098	0.76	-2.9100	2.8090	0.92
	(0.697)	(0.299)	(40)	(0.289)	(0.179)	(23)
Range of predictor variables	min.	max.		min.	max.	
HT [in cm]	6.0	252.0		18.0	106.0	
ln(HT)	1.808	5.529		2.890	4.663	
BD [in mm]	4.5	39.0		2.2	10.0	
ln(BD)	1.504	3.664		0.788	2.303	

Table 4.7: Multiple regression analysis of current annual growth (CAG) of *Corylus cornuta* and *Amelanchier alnifolia* in some aspen forest stands.

Species Location Stand	regression equation	R^2	N
Corylus cornuta			
1. Independent variable list: ln(LB), ln(BD), ln(HT), ln(AGE).			
Quarter Potr-6	ln(CAG) = 0.5390ln(LB) - 1.0323ln(AGE) + 0.9776ln(BD) + 0.5278ln(HT) -3.3414	0.73	77
Potr-2	ln(CAG) = 1.6975ln(BD) - 1.0605ln(AGE) + 0.3322ln(LB) - 2.0967	0.70	54
Sanctuary Potr-1	ln(CAG) = 1.2059ln(HT) - 1.1795ln(AGE) + 0.6058ln(LB) - 4.4625	0.75	60
2. Independent variable list: ln(BD), ln(HT), ln(AGE).			
Quarter Potr-6	ln(CAG) = 0.8844ln(HT) - 0.9470ln(AGE) + 1.5964ln(BD) -5.8952	0.68	77
Potr-2	ln(CAG) = 2.3926ln(BD) - 0.9705ln(AGE) - 3.3928	0.67	54
Sanctuary Potr-1	ln(CAG) = 1.2833ln(HT) - 1.0261ln(AGE) + 1.5727ln(BD) - 7.4834	0.75	60
Amelanchier alnifolia			
1.Independent variable list: ln(LB), ln(BD), ln(HT), ln(AGE).			
Quarter Potr-6	ln(CAG) = 0.6994ln(LB) - 0.9095ln(AGE) + 1.3178ln(BD) - 1.5981	0.88	28
Sanctuary Potr-1	ln(CAG) = 1.0270ln(LB) - 1.0743	0.64	25
2. Independent variable list: ln(BD), ln(HT), ln(AGE).			
Quarter Potr-6	ln(CAG) = 3.0152ln(BD) - 1.4041ln(AGE) - 4.1598	0.83	28
Sanctuary Potr-1	ln(CAG) = 1.9765ln(BD) - 3.9499	0.63	25

stand. In the stands Potr-2 and Potr-1 the first independent variables were basal diameter and height, respectively.

In every stand, logarithmically transformed age was the second variable chosen for the equation from both independent variable lists. This variable explained 10-16% of the total variation of current annual growth as compared to an additional 3-5% explained by any of the third independent variables. In all equations, the regression coefficient for age was negative indicating a decrease of current annual growth with age among plants of similar size.

The third predictor variable in the stands Potr-1 and Potr-2 was leaf biomass. For the stand Potr-6, two more independent variables were significant: height and basal diameter. Without leaf biomass in the independent variable list, basal diameter was included in the regression equation for the stands Potr-6 and Potr-1. No third predictor variable was selected for the stand Potr-2.

High correlations among basal diameter, height and leaf biomass in each stand were noted. However, a poor correlation of these variables to age was found. Thus, only one of them is of primary importance for the regression model, while the inclusion of age explains much additional variation. A sample regression surface of the two most important predictor variables is shown in Figure 4.17.

A multiple regression analysis was also performed on the current annual growth of *A. alnifolia*. Similar equations to those for *C. cornuta* were obtained for the stand in the quarter section. Leaf biomass or basal diameter were selected in the first step. Age was the second variable selected. It explained an additional 8-23% of the variation of current annual growth. Again the regression coefficient was negative for age.

A different result was obtained for the stand Potr-1 in the sanctuary. No second variable could explain a significant amount of the residual variation. So the multiple regression equation remained the same as the equation found in the simple regression analysis.

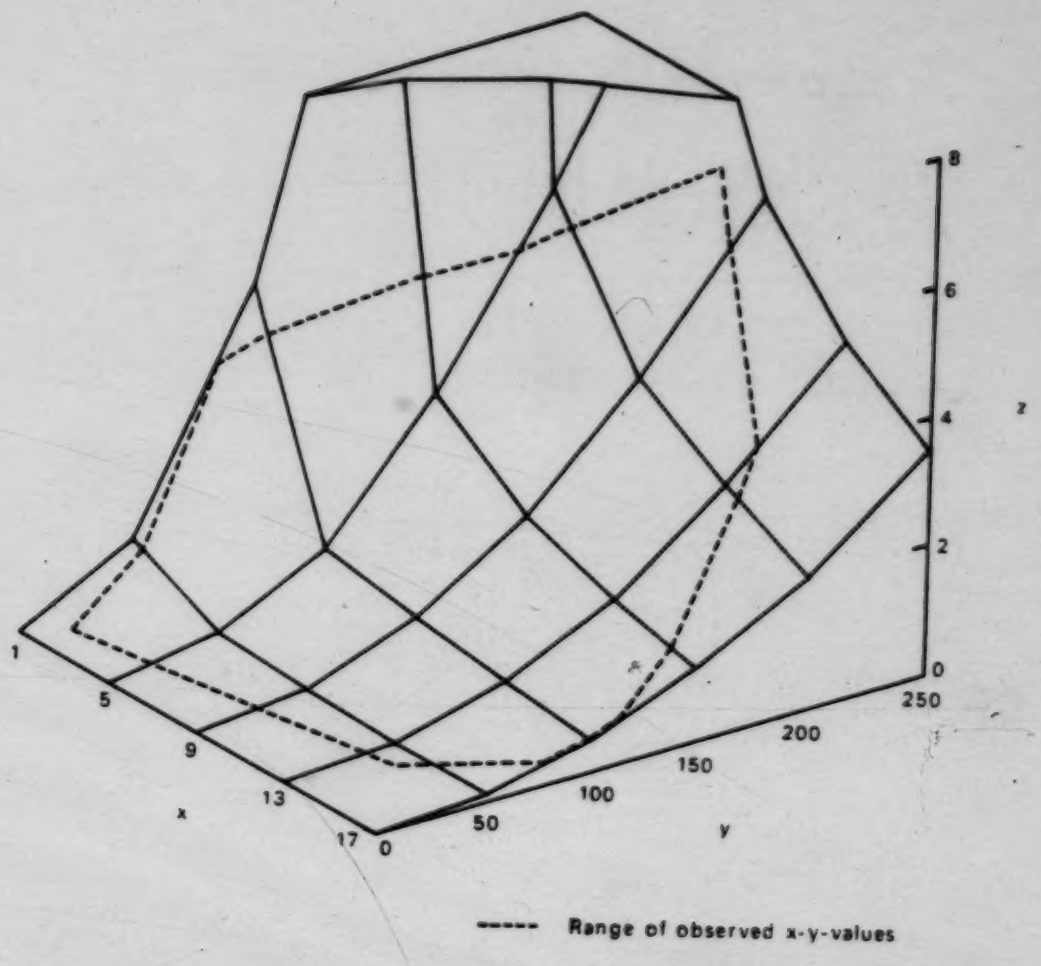

Figure 4.17: Multiple regression surface of current annual growth of *Corylus cornuta* (in g dry-weight on the z-axis) in the stand Potr-1 on the height (in cm on the y-axis) and the age (in years on the x-axis) of stems.

4.2.3.4 Unit area biomass comparison

The results of the analysis of area based biomass measurements are shown in Table 4.8. The one-way analysis of variance found real differences in the production of current annual growth among the stands. The multiple comparison procedure showed that the mean in the stand Potr-6 was significantly greater than the means of the other two stands. The analysis of variance had also shown highly significant differences in the densities and basal areas of *C. cornuta* stems in the three stands.

The densities measured in the community survey were consistently lower than the ones from the biomass quadrats. The estimates were obtained from a total sample area of 40 m^2 in the plant community survey as compared to 3 m^2 in the biomass sampling. With a larger sample number (i.e. number of quadrats) and a larger total sample area the plant community survey data provide better estimates of the population densities. The strong bias towards high densities probably resulted in an overestimate of the area-based biomass measurements. However, as in the community survey, densities within the stands in the quarter section were higher than in the stand Potr-1 in the sanctuary.

The multiple comparison of stand means of density and basal area (Table 4.8) showed that the basal area in the stand Potr-6 was significantly higher than in the two other stands. On the other hand, the densities of the stands Potr-6 and Potr-2 were very similar. The stem density of *C. cornuta* was much lower in the stand Potr-1.

A relationship between biomass and density or basal area was expected. The variables were plotted on double log paper (Figure 4.18). The correlation between biomass variables was the highest with basal area. Although the relationship is curvilinear on the double log-scale, it is almost linear over the range of basal areas of the samples. This suggested an adjustment for the differences of basal area among the samples with a analysis of covariance of logarithmically transformed data. Highly significant differences among stands were found with this procedure for leaf biomass only (Table 4.9). The mean of leaf biomass adjusted for basal area was much higher in the stand Potr-1 and it was

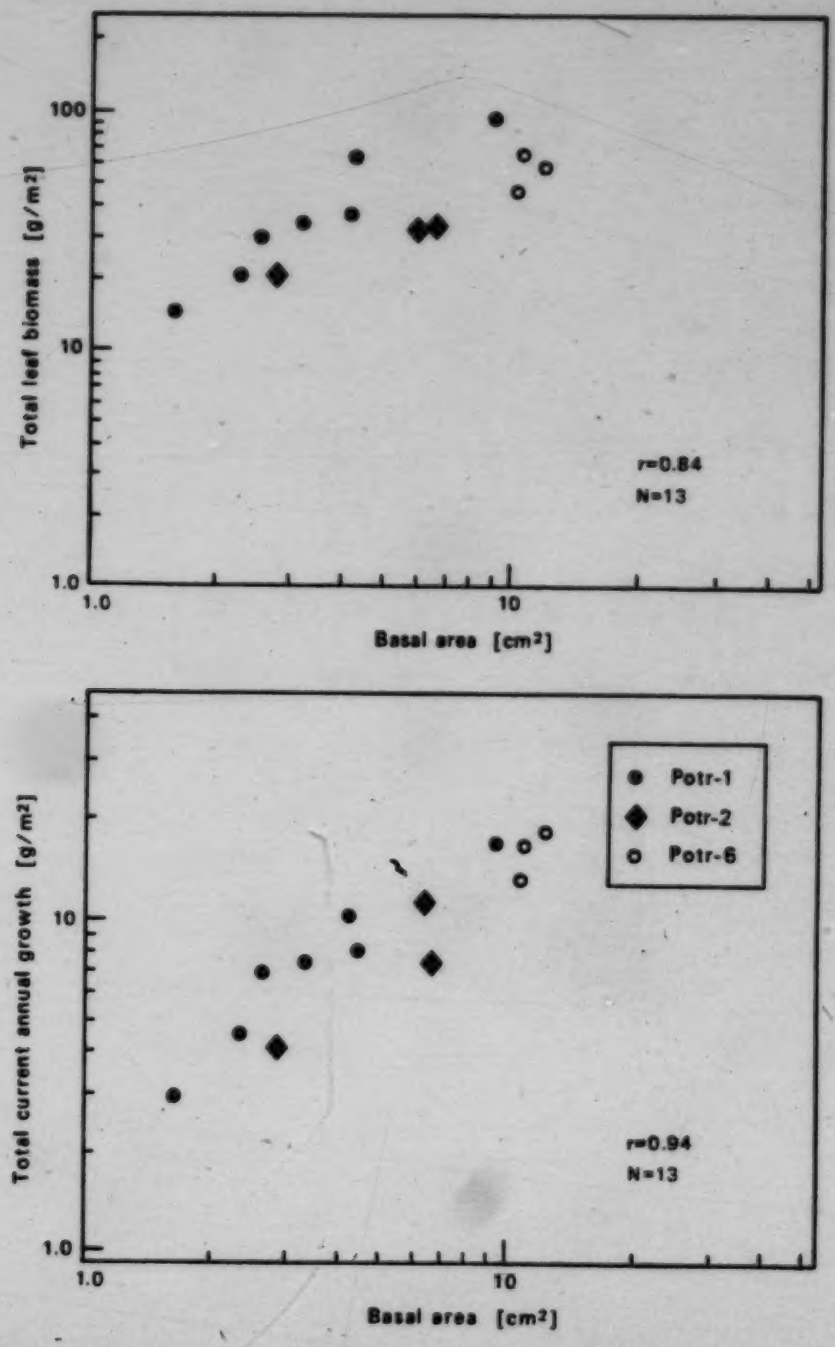

Figure 4.18: Relationship of unit-area biomass samples of *Corylus cornuta* to basal area.

Table 4.8: Multiple comparison of stand means of area-based biomass measurements of *Corylus cornuta*.

VARIABLE			descriptive statistics			one-way ANOVA of stands		
Location	Stand	MC[1]	mean	standard error	N	F	degrees of freedom	sign.
LEAF BIOMASS [in g/m²]						1.167	(2,10)	n.s.
Quarter	Potr-6	a	57.5	4.21	3			
"	Potr-2	a	29.8	4.56	3			
Sanctuary	Potr-1	a	41.9	10.61	7			
CURRENT ANNUAL GROWTH [in g/m²]						4.861	(2,10)	P<0.03
Quarter	Potr-6	a	16.2	1.53	3			
"	Potr-2	b	7.7	2.11	3			
Sanctuary	Potr-1	b	8.0	1.70	7			
TOTAL ABOVEGROUND BIOMASS [in g/m²]						1.976	(2,10)	n.s.
Quarter	Potr-6	a	420.0	58.81	3			
"	Potr-2	a	197.3	35.23	3			
Sanctuary	Potr-1	a	232.3	70.32	7			
BASAL AREA [in cm²/m²]						10.617	(2,10)	P<0.0034
Quarter	Potr-6	a	11.2	0.56	3			
"	Potr-2	b	5.3	1.23	3			
Sanctary	Potr-1	b	4.0	1.00	7			
DENSITY [in 1/m²]						9.909	(2,10)	P<0.0042
Quarter	Potr-6	a	25.7	1.45	3			
"	Potr-2	a	23.0	6.81	3			
Sanctuary	Potr-1	b	8.0	1.53	7			
DENSITY [in 1/m²] (from community survey)								
Quarter	Potr-6		8.6	4.30	10			
"	Potr-2		7.9	1.24	5			
Sanctuary	Potr-1		4.6	2.34	10			

[1]Multiple comparison: Means with the same letter are not different from each other at P<0.05.

Table 4.9: Analysis of covariance of logarithms of area-based biomass samples of *Corylus cornuta*.

VARIABLE	Stand	N	observed mean	adjusted mean	comparison of adjusted means	significance of ANCOVA stand effect	significance of ANCOVA covariate: ln(BA)
ln(CAG)						n.s.	P<0.005
	Potr-6	3	2.77	1.99			
	Potr-2	3	1.95	1.95	a		
	Potr-1	7	1.95	2.28	a		
ln(LB)						P<0.006	P<0.005
	Potr-6	3	4.05	3.23	a		
	Potr-2	3	3.37	3.36	a		
	Potr-1	7	3.56	3.90	b		
ln(TB)						n.s.	P<0.005
	Potr-6	3	6.02	5.03	a		
	Potr-2	3	5.25	5.24	ab		
	Potr-1	7	5.19	5.61	b		

significantly different from the means of the two stands in the quarter section.

4.2.4 Discussion

4.2.4.1 Population ecology of shrubs

The difficulty with attempting to delineate individuals of vegetatively regenerating plants provides problems for the investigation of plant population dynamics (Harper 1977). Clones of *C. cornuta* are the genetically distinct individuals of this shrub species. Field observations demonstrated that these clones are interwoven so that they cannot be distinguished without excavation. In this study, the individual stems of *C. cornuta* or *A. alnifolia* were considered to be the fundamental unit of the *C. cornuta* population in a stand. The stems of a clone are interconnected by underground structures. Interactions of vegetative shoots of the same plant have been demonstrated for some herbaceous species (Ashman *et al.* 1982, Noble and Marshall 1983). However, a pragmatic definition of a population as an assemblage of structural units, also called modules, can be meaningful (White 1979). The aerial shoot or stem in the investigated shrub species was clearly the module of interest.

The crucial demographic statistics of the rates of age-specific survival and reproduction are difficult to measure for long-lived species. It has been demonstrated that these rates are dependent on the size and density of plants (Crawley 1983). Age structure diagrams can be constructed for perennial plants if their age can be determined from growth rings. Under constant conditions (i.e. constant rates of production and mortality with time), the population will assume a stable age distribution reflecting the age-specific mortality pattern (Ricklefs 1979). Such distributions have been documented for some trees in mature forests (Whittaker 1970). If the rates of survival and reproduction change with time, as expected with a change in browsing intensities, a variety of age distributions can result. Further, different combinations of the rates of mortality and reproduction can produce the same age structure. As detailed data on mortality and reproduction are not

available, the interpretation of the age structures of *C. cornuta* has to remain tentative.

C. cornuta stems have been described as having a well-defined maximum life span of approximately seventeen years (Buckmann 1964). This corresponds well with the findings at Ministik. Thus, the stand origin dates (i.e. 1937) suggested by tree ages (48 years) and the age of *C. cornuta* stems were quite different. It was attempted to get clues on *C. cornuta* stem mortality by counting dead stems during the plant community survey. However, few dead stems were found; accounting for less than five per cent of the total number of *C. cornuta* stems. No differences were found among stands. It appears that the mortality of medium to large stems is low. The mortality of new sprouts cannot be assessed, because it must be assumed that these decay quickly if they die. No other clues on the mortality pattern of *C. cornuta* were found.

More information is available on the reproductive ecology of *C. cornuta*. In Minnesota pine forests, Tappeiner *et al.* (1979) found many seedlings of *C. cornuta* filling in open space among extending established clones. When *C. cornuta* cover became almost continuous, few seedlings were recorded. It appears, that the upland forest communities studied in Ministik were already at this later stage. No seedlings of *C. cornuta* which had germinated in the year 1983 were encountered in the study sites.

Investigations of Tappeiner (1971) and this study have shown that stems of *C. cornuta* go through three quite distinct stages in their life cycle. Approximately seven years are required for the growth and establishment of a mature stem. Once a stem reaches maturity it starts to produce underground stems whose extension may again involve several years. New stems are produced this way by vegetative reproduction. Finally, as a stem approaches the maximum life span, it becomes stagnant and finally dies.

Surprisingly, no tendency for a strong increase in stem density since the establishment of the MWRS was found in the age structures of the stands in the quarter section. A high proportion of young stems typical for a growing population was not obvious. The age structure in the stand Potr-1 displayed a slightly increasing trend.

However, the plant community survey had revealed that the density of *C. cornuta* stems was 50% higher in the quarter than in the sanctuary (Table 3.2). The higher density of *C. cornuta* stems in the quarter section may be a result of earlier human land use. The *C. cornuta* in the quarter section may already approach an upper density limit. The still increasing *C. cornuta* stem population in the stand Potr-1 may be related to the lower stem density in this stand which leaves more room for population growth.

The age structures of *A. alnifolia* are very inconclusive. The obvious difference to *C. cornuta* is the greater lifespan. The oldest stems of *A. alnifolia*, which reach well beyond the maximum foraging height of elk and moose, date back to the stand origin. The small sample size did not allow the construction of the detailed age structure necessary for the evaluation of recent changes in population dynamics. With five year age classes, the two age structures do not display any obvious differences. The frequency of stems seems to decline steadily with increasing age.

Most concepts in population ecology, mainly developed from studies of animals, may not readily be transferred to plant populations. One major problem of applying demographic analysis to plant species is their phenotypic plasticity (Harper 1977). Conditions of the environment, physical and biological, rather than the actual age largely control the growth of a long-lived plant. Consequently, the correlation between size and age is often weak. The age structure of *C. cornuta* and *A. alnifolia* insufficiently describe the stem populations of these species (Gatsuk 1980). The size a stem may reach in a given time, and thus its productivity, is controlled by factors limiting its growth. Competition with stems or shoots of its own or other species may restrict the growth of the members of the stem population. Feeding by herbivores on the stems can be another limiting factor. Therefore, the frequency distributions of size and biomass attributes yield further insights into the present state of these populations.

Noticeable differences were found in the physiognomy of stems of *C. cornuta*. Stems of this species seemed to reach a maximum height of only 140-150 cm in the quarter

section. This limit represents the browse line, a phenomenon easily observed in the field. A second major impact on the morphology of stems was displayed by the crown area histograms. The range of the crown areas of *C. cornuta* in the quarter section was confined. The frequent browsing on twigs prevented the development of wide-spreading branches. Almost all shrubs in the quarter were severely hedged with short branches concentrated around the primary stem. The stem diameter distributions also indicate that the stems in the quarter section did not reach the extreme sizes of stems in the sanctuary. The browsing appears to have reduced secondary stem growth near the base (Farrar 1961).

The shape of the graph of the basal diameter distribution (Figure 4.4) indicates that the stem population in the stand Potr-1 was primarily made up of small individuals. These included young sprouts as well as old, suppressed stems. Only a few stems have grown to a large, dominant size. The distribution of basal diameters in the stand Potr-6 is skewed to the opposite side. Presumably, browsing prevented the development of dominant stems. This released somewhat the interspecific competition, which is commonly the limiting factor for growth at high population densities (Crawley 1983). Young and suppressed stems could grow at a more rapid rate until they reached the limit set by browsing. The resulting size structure involves many plants of intermediate size and fewer small stems. The stem population in the stand Potr-2 appeared to be in an intermediate phase where basal diameters were approximately normally distributed.

The cut-off phenomenon was also observed in the biomass distributions. Browsing definitely imposed upper limits on the growth of *C. cornuta* in terms of stem morphology as well as in terms of production of new tissues and accumulation of woody biomass. The normal growth of shrubs was retarded by this heavy herbivore use (Milner 1977). For two reasons, these limits were less apparent for *A. alnifolia*. The maximum height and age a stem of *A. alnifolia* can reach is greater. Hence, some stems had grown beyond the range of accessibility to browsing ungulates prior to the establishment of MWRS. Secondly, *A. alnifolia* is a much preferred forage species. In contrast to *C. cornuta*, it has been utilized

in the sanctuary to a greater extent.

An evaluation of site differences without environmental measurements is problematic. The mean most variables (i.e. leaf biomass, current annual growth, total aboveground biomass and basal diameter) were lower in the stand Potr-2 than in the other two stands. The mean dbh of aspen is also lowest in the stand Potr-2. Given similar stem densities for trees as well as shrubs, the consistently lower central tendencies of these variables provide the only indication of a difference in site qualities.

4.2.4.2 Growth dynamics

The change of productivity with time is termed growth dynamics. Frequently, growth patterns of short-lived plants or plant parts are analyzed throughout a growing season. The growth of perennial plants can vary greatly from year to year. Aging of plants and various environmental conditions influence these fluctuations. With woody perennials, indirect estimates of past productivity can be obtained. Horizontal and vertical patterns of ring width may yield reliable indications of growth dynamics (Farrar 1961).

The age-specific growth pattern was analyzed by plotting size or biomass attributes of a stem against stem age. The poor relationships between these variables indicate the great variability from plant to plant. The broad scattering further suggests that factors other than calender age largely determine the size a stem will reach in a given time span.

The great variability around the average trends illustrates that a stem may follow a continuous range of pathways. Its growth may be suppressed by the environmental conditions or by competition with other plants. These stems may be found at the lower part of the diagrams. On the other hand, a stem may be very vigorous if conditions are favorable. There is a continuum between these two extremes where the majority of stems can be found. It is possible that a change in the environmental conditions may cause a stem to alter its position between the extremes.

The ranges of size and biomass of stems within an age class can largely be set by the site. It is most significant that the upper ranges of all variables are much reduced in the

quarter section. This is an age-specific manifestation of the cut-off effect observed in the frequency distributions.

4.2.4.3 Comparison of shrub productivity

Three variables served as indicators for the productivity of shrub stems. Leaf biomass is a measure of a summer forage resource. The leaves of *C. cornuta* and *A. alnifolia* comprise 10 to 20% of the summer diet of wapiti in the forest communities (Nietfield 1983). Leaf biomass also represents the photosynthetic capacity of a stem. Leaf area, which is related to the extent of potential uptake of CO_2 and the amount of light interception, is highly correlated with the leaf biomass of *C. cornuta*. A reduction of leaf biomass means a decrease in the production and accumulation of photoassimilates.

The current annual growth signifies to some degree the current year's production of winter forage. As numerous factors may influence the amount of new twig material produced, it may be regarded as an average index of the vigour of a stem. It does not represent the total forage resource, because older branches of a shrub may be consumed as well. However, during the cold season the new twigs are the most nutritious and the most preferred parts of the plant. Some of the current annual growth of severely hedged shoots may not be easily accessible to browsers. The tedious sampling of current annual growth remains the most practical method in ungulate management to assess winter forage production of shrubs.

The total aboveground biomass of a stem is the result of the accumulation of woody matter over several years. The age of a stem presents the time unit over which the production of aboveground woody biomass is measured. Year to year variations of growth are integrated by this variable. Except for the first few years the weight of stems and branches is the major component of the aboveground biomass of shrubs. Whittaker (1962) thought that the shrub physiognomy was limited by a ratio of active photosynthetic tissues to the supporting woody biomass. Total aboveground biomass is less significant for forage quantity analysis than the other two variables.

The techniques for biomass measurements can be divided into two basic approaches (Rutherford 1979). In the plant-based techniques a specific local relationship between mass and one or more predictor variables (e.g. size parameters) is established. Subsequently an inventory of the predictor variable(s) yields estimates of biomass. A comparison of the parameters in the relationship was performed in this study to evaluate differences caused by browsing. An inventory of the predictor variable was not done. In a second approach here referred to as the area-based or unit-area approach, biomass was sampled directly in plots of known size. Unlike the plant-based approach, these techniques are destructive and cannot be repeated for the same plot.

In the plant-based approach, the relationships between biomass and predictor variables were established by linear regression analysis of logarithmically transformed data. The significant differences in the slopes of the regression lines for *C. cornuta* indicate smaller increments of leaf biomass and current annual growth at a given size increment in the heavily browsed quarter section. However, the plot of the regression lines (Figure 4.16) also illustrates that below the point of intersection the production of leaf biomass and current annual growth are higher in the heavily browsed stands than in the sanctuary. This means that plants may actually be more vigorous as they start growing. As they approach a certain critical size limit, however, they became severely suppressed as a result of foraging herbivores. The critical height lies somewhere below the browse-line, because ungulates forage well below this conspicuous line. Especially during the first winter, sprouts may be protected by the snowpack.

Although the slopes of the simple linear regression lines of *A. alnifolia* are slightly larger for the stand in the sanctuary, they are not significantly different (Table 4.5). As already mentioned, this shrub species is heavily foraged on in both stands. Thus the productivity of *A. alnifolia* stems may be the same in these stands.

For leaf biomass and total aboveground biomass, height and basal diameter are almost equally well suited as predictor values for both species. The correlation between

production of current annual growth and the plant dimension is weak. Whereas leaf and total biomass can be estimated with reasonable accuracy with the plant-based approach, large confidence limits must be accepted for the current annual growth.

In many cases, leaf biomass would have been included as the first variable in the multiple regression equation. Its correlation to current annual growth was similar to the size parameters (Table 4.4). The rapidly extending shoots of shrubs frequently utilize carbohydrates produced and stored during the previous growing season (Kozlowski and Keller 1966). If the leaf weights of a stem in two successive years are correlated, the current leaf biomass may also indicate the potential accumulation of photoassimilates of the previous year. These intercorrelations may partly explain the relationship between the production of new twig material and leaf biomass.

The fact that age is negatively correlated to current annual growth in the multiple regression equation (Table 4.7) throws new light on the growth dynamics of *C. cornuta*. It shows that among plants of equal size the production of new twig material decreases with age. The same pattern was found for *A. alnifolia* in the quarter section. It remains unclear, why this pattern was not found in the multiple regression analysis of the current annual growth for this species in the sanctuary.

The inclusion of further predictor variables in the equation greatly improved the regressions on current annual growth of *C. cornuta*. However, the age of a stem, the variable which accounted for most of the additionally explained variance, cannot easily be determined in the field. It will be of little practical value for biomass inventories with the plant-based approach.

The value of the results of the area-based approach was limited in this study, because sample size was small (N=3 to 7). No definite effects of browsing on the productivity of *C. cornuta* in a unit area could initially be shown. The significantly different densities and basal areas raised the question of the representativeness of the samples. As a consequence of the bias of most quadrats toward high stem densities the

sample means were not a valid estimate of the stand mean.

A relationship between the number of plants and the biomass per unit area has been frequently found (Harper 1977). With increasing density the biomass approaches an upper limit probably representing the limit of productivity set by the site. Such a relationship was found for *C. cornuta*. For this perennial shrub the relationship was improved when density was replaced by basal shrub area (Figure 4.18), because the density did not take the size distributions of the stems into account. Again, the small sample number did not allow an evaluation of browsing effects on this relationship (i.e. whether the slope of biomass increase with basal area remains the same under different browsing intensities).

Under the assumption that the same relationship holds for all the stands, the basal area was used as a covariate. If adjusted for basal area, it was found that differences in leaf biomass among stands were highly significant (Table 4.9). The leaf biomass was significantly higher in the lightly browsed stand Potr-1. No significant difference was found for current annual growth with the analysis of covariance. It must be realized that the adjustment of stand means to the overall covariate mean (i.e. mean basal area of all samples) standardizes the biomass measurements from a unit area to a unit basal area. Thus it modified the area-based approach.

The positive correlation of biomass and density (and basal area) demonstrated that productivity can be increased by an increase in the vigour of individual stems as well as by an increase in the number of plants. A definite density increase of *C. cornuta* stems had been found in the community survey. Shrubs can compensate for biomass loss to foraging herbivores in two ways. The invigourating effect of browsing may increase the productivity of individual stems. The shrubs may also compensate for losses on the population level (Crawley 1983). The population size may be increased through more frequent sprouting from underground stems.

4.2.5 Conclusion

In this section, the growth dynamics of selected tall, single-stemmed (as opposed to clumped) shrubs dominating a boreal forest ecosystem were analyzed. Although the field work was carried out over one season only, some information concerning the dimension of time was made available by aging shrub stems. As in many plant ecological studies, it was found that growth was not closely related to the age of the plant modules because many other factors influence the course of their development.

The developmental stage of a plant can be recognized from morphological characteristics (Gatsuk 1980). In this study at Ministik, biomass and size attributes were used to describe shrub stems quantitatively. The total aboveground biomass and the leaf biomass increased rapidly with size. Size parameters are an appropriate indicator of the vigour (or the degree of suppression) of shrub stems with the same age. Many factors influence plant size. On a geographical scale climate may be the important factor limiting growth. On the local scale, within a particular habitat type, other factors are responsible for the great variability in the growth (referred to as phenotypic plasticity) of the members of a plant population. Density of plants has been found to be a limiting factor (e.g. Yoda *et al.* 1963). At the MWRS the heavy browsing by native ungulates presents an upper limit to growth.

It is difficult to separate the annual biomass increment of shrubs from earlier growth. A variable portion of shrub production is the current annual growth. A descriptive model of the production of new twigs of *C. cornuta* stems was developed by regarding a multiple regression equation as a surface in three-dimensional space. This model visualizes the way that plant productivity is related to size as well as age. It illustrates that both variables are needed to classify the perennial plant with regard to its productivity.

The production of current annual growth is a good measure of the quantity of winter forage available to browsing ungulates. Repeated heavy browsing was found to restrict the productivity of large, mature *C. cornuta* stems in the quarter section of the MWRS. However, the higher stem density compensated for the reduced vigour to some degree. Thus, no

difference in *C. cornuta* production on a unit-area basis may be found between the two grazing systems.

Most preferred forage shrubs in the forest communities (*A. alnifolia*, *C. stolonifera*, *Prunus* spp., *V. edule*) were rare and/or have decreased in the quarter section. Along with the suppression of their productivity by browsing, this severely limits the quantity and the quality of forage available to browsing ungulates. However, it appeared that the growth of these shrubs was also retarded in the sanctuary.

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Appendix 1: Domin scale - transformation scale for the ordination of plant community data.

Per cent cover value	transformed cover value
0	1
1	2
3	3
8	4
16	5
30	6
42	7
68	8
88	9
100	10

All other cover values are calculated with linear interpolation (Source: Hill 1979).

Appendix 2: List of species encountered during the plant community survey (Nomenclature follows Packer 1983).

Species name	Common name	Code
TREES:		
Populus balsamifera	balsam poplar	POBA
Populus tremuloides	aspen	POTR
Betula papyrifera	paper birch	BEPA
SHRUBS:		
Amelanchier alnifolia	saskatoon	AMAL
Corylus cornuta	beaked hazel	COCO
Cornus stolonifera	red osier dogwood	COST
Lonicera dioica	twining honeysuckle	LODI
Lonicera involucrata	bracted honeysuckle	LOIN
Prunus pensylvanica	pin cherry	PRPE
Prunus virginiana	choke cherry	PRVI
Ribes americanum	wild black currant	RIAM
Ribes glandulosum	skunk currant	RIGL
Ribes oxycanthoides	wild gooseberry	RIOX
Ribes triste	wild red currant	RITR
Rosa acicularis	prickly rose	ROAC
Rubus idaeus	raspberry	RUID
Shepherdia canadensis	buffaloberry	SHCA
Salix arbusculoides	willow	SXAR
Salix bebbiana	Bebb's willow	SXBE
Salix discolor	pussy willow	SXDI
Salix planifolia	willow	SXPL
Salix pseudomonticola	willow	SXPS
Salix pyrifolia	willow	SXPY
Salix serissima	willow	SXSE
Symphoricarpos albus	snowberry	SYAL
Symphoricarpos occidentalis	buckbrush	SYOC
Viburnum edule	low bush cranberry	VIED
FORBS:		
Achillea millefolium	yarrow	ACMI
Actaea rubra	baneberry	ACRU
Aralia nudicaulis	wild sarsparilla	ARNU
Aster borealis	aster	ASBO
Aster ciliolatus	Lindley's aster	ASCI
Aster conspicuus	showy aster	ASCO
Aster puniceus	purple-stemmed aster	ASPU
Cirsium arvense	thistle	CIAR
Cornus canadensis	bunchberry	COCA
Disporum trachycarpum	fairy-bell	DITR
Epilobium angustifolium	fireweed	EPAN
Erigeron philadelphicus	fleabane	ERPH

Appendix 2 - continued.

Fragaria vesca	strawberry	FRVE
Fragaria virginiana	strawberry	FRVI
Galeopsis tetrahit	hemp nettle	GATE
Galium boreale	bedstraw	GABO
Galium trifidum	bedstrw	GATE
Galium triflorum	sweet bedstraw	GATR
Geum allepicum	yellow avens	GEAL
Habenaria hyperborea	northern green orchid	HAHY
Heracleum lanatum	cow parsnip	HELA
Hieracium umbellatum	hawkweed	HIUM
Juncus balticus	rush	JUBA
Lathyrus ochroleucus	pea vine	LAOC
Lathyrus venosus	pea vine	LAVE
Linnaea borealis	twinflower	LIBO
Lysimachia thyrsiflora	loosestrife	LYTH
Maianthemum canadense	wild lily-of-the-valley	MACA
Mentha arvense	common mint	MEAR
Mertensia paniculata	bluebell	MEPA
Mitella nuda	bishop's cap	MINU
Orthilia secunda	wintergreen	ORSE
Osmorhiza depauperata	sweet cicley	OSDE
Parnassia palustris	grass-of-Parnassus	PAPA
Petasites palmatus	coltsfoot	PEPA
Petasites sagittatus	coltsfoot	PESA
Polygonum amphibium	water smartweed	POAM
Potentilla anserina	silverweed	POAN
Potentilla norvegica	rough cinquefoil	PONO
Pyrola asarifolia	common pink wintergreen	PYAS
Pyrola chlorantha	wintergreen	PYCH
Rubus arcticus	dwarf raspberry	RUAR
Rubus pubescens	dewberry	RUPU
Smilacina stellata	Salomon's seal	SMST
Solidago canadensis	goldenrod	SOCA
Sonchus arvensis	sow thistle	SOAR
Stachys palustris	hedge nettle	STPA
Stellaria spp.	chickweed	STEL
Taraxacum officinale	dandelion	TAOF
Trifolium repens	white clover	TRRE
Urtica gracilis	common nettle	URGR
Vicia americana	vetch	VIAM
Viola canadensis	violet	VICA

GRAMINOIDS:

Calamagrostis canadensis	bluejoint	CACA
Calamagrostis inexpensa	northern reed grass	CAIN
Carex atherodes	sedge	CXAT
Carex aurea	sedge	CXAU
Carex bebbii	sedge	CXBE
Carex disperma	sedge	CXDI
Carex rostrata	sedge	CXRO

Appendix 2 - continued.

Glyceria striata	fowl manna grass	GLST
Oryzopsis asperifolia	rice grass	ORAS
Phalaris arundinacea	reed canary grass	PHAR
Poa spp.	bluegrass	POAS
Schizachne purpurascens	false melic	SCPU
PTERIDOPHYTES:		
Botrychium lunaria	moonwort	BOLU
Dryopteris sp.	fern	DRYO
Equisetum arvense	common horsetail	EQAR
Equisetum scirpoides	horsetail	EQSC
Equisetum sylvaticum	woodland horsetail	EQSY

Appendix 3: Mean cover (in per cent) of vascular plant species in the study sites.

SPECIES	ASPEN FOREST					BALSAM POPLAR FOREST						SHRUB FEN		
	Potr-1 N=10	Potr-5 N=10	Potr-2 N=5	Potr-3 N=5	Potr-6 N=10	Poba-1 N=5	Poba-2 N=5	Poba-4 N=10	P-1 N=10	P-3 N=5	P-4 N=5	Will-2 N=14	Will-3 N=9	Will-4 N=9
Trees:														
POTR	42.90	29.50	55.60	23.80	44.70	5.60	15.60	0.30	27.10	4.00	6.64	1.38	0.03	0.50
POBA	1.00	4.90	0.0	0.0	3.30	39.80	32.60	48.70	18.80	49.80	39.40	5.30	1.34	5.50
BEPA	0.0	0.0	0.20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.31	2.41	0.51
Shrubs:														
AMAL	2.51	4.11	1.24	0.80	1.82	0.40	0.02	0.62	0.19	0.0	1.64	0.17	0.01	0.0
COCO	25.20	17.90	21.80	44.20	28.20	1.60	0.80	0.21	0.0	0.0	0.0	0.0	0.01	0.0
COST	0.60	0.10	0.0	0.62	0.41	1.80	3.02	1.70	1.26	0.40	1.80	0.29	0.12	0.26
LODI	1.60	0.33	0.22	0.02	0.42	1.60	1.22	0.70	0.25	0.0	0.62	0.01	0.02	0.0
LOIN	0.31	0.40	0.60	0.40	1.20	4.20	7.60	15.50	2.33	5.40	14.80	1.64	3.70	1.25
PRPE	0.0	1.31	0.01	0.42	0.0	0.0	0.0	0.10	0.75	0.0	0.0	0.0	0.0	0.0
PRVI	3.21	0.50	0.0	0.02	0.70	0.20	0.0	2.30	0.25	0.0	1.00	0.0	0.0	0.0
RIAM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.83	1.20	0.0	0.0	0.10	0.0
RIGL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.34	0.0	0.0	0.0	0.0	0.0
RIOX	0.0	0.0	0.44	0.02	0.40	0.0	6.22	0.25	5.25	4.02	10.80	0.29	0.51	1.00
RITR	0.01	0.01	0.42	0.02	0.20	3.80	2.00	0.40	1.67	0.02	0.02	0.0	0.0	0.0
ROAC	4.30	1.14	3.00	5.00	5.11	1.84	2.60	0.20	2.09	0.02	4.40	0.09	0.50	0.0
RUID	0.0	0.10	0.22	1.82	2.70	0 80	12.20	1.71	13.70	2.00	1.42	3.94	2.01	1.15
SHCA	0.0	0.0	0.0	0.20	0.0	0.0	0.20	0.0	0.0	0.0	0.0	0.14	0.0	0.0
SXAR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.58	1.10	3.75
SXBE	0.0	0.20	0.0	0.0	0.0	0.0	0.0	0.81	0.0	0.0	0.0	0.71	0.40	0.0
SXDI	0.0	0.0	0.0	0.0	0.0	0.0	2.60	0.0	0.0	0.0	0.20	0.01	0.50	0.0
SXPL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.40	11.20	26.00
SXPS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.14	0.50	2.25
SXPY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.93	1.42	0.0
SXSE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.14	0.0	0.0
SYAL	1.71	0.36	3.80	1.62	4.50	0.40	0.26	4.51	1.67	0.20	0.40	0.15	0.0	0.0
SYOC	0.0	0.0	0.0	0.0	0.50	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.50	0.0
VIED	1.41	1.80	0.80	0.0	0.12	0.60	1.00	0.01	0.0	0.0	0.0	0.0	0.0	0.0
Forbs:														
ACMI	0.0	0.0	0.0	0.0	0.0	0.02	0.0	0.0	0.0	0.0	0.0	0.01	0.11	0.0
ACRU	0.22	0.0	0.02	0.0	0.01	0.02	0.02	0.21	0.03	0.0	0.20	0.0	0.0	0.0
ARNU	9.70	10.30	3.80	2.40	0.50	27.40	15.60	24.00	1.68	0.0	4.00	0.0	0.01	0.0
ASBO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05	0.02	0.01
ASCI	1.22	1.12	1.20	1.42	1.13	1.20	0.62	1.23	1.25	0.06	0.46	0.01	0.10	0.01
ASCO	0.61	0.22	0.0	0.62	0.02	0.0	0.02	0.31	0.0	0.0	0.0	0.0	0.0	0.0
ASPU	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.54	0.04

Appendix 3 - continued.

SPECIES	ASPEN FOREST					BALSAM POPLAR FOREST						SHRUB FEN		
	Potr-1 N=10	Potr-5 N=10	Potr-2 N=5	Potr-3 N=5	Potr-6 N=10	Poba-1 N=5	Poba-2 N=5	Poba-4 N=10	P-1 N=10	P-3 N=5	P-4 N=5	Will-2 N=14	Will-3 N=9	Will-4 N=9
Forbs:														
CIAR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.58	1.20	0.0	0.27	0.64	0.16
COCA	1.90	3.00	2.80	3.40	0.51	1.20	0.0	0.63	0.67	0.0	0.40	0.0	0.01	0.14
DITR	0.71	0.82	0.60	0.02	0.30	0.60	0.82	0.33	0.09	0.0	0.0	0.0	0.0	0.0
EPAN	1.11	0.43	0.0	0.0	0.0	1.04	1.82	2.22	0.02	0.01	0.0	0.0	0.10	0.52
ERPH	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.01	0.0
FRVE	0.0	0.0	0.0	0.0	0.10	0.0	0.0	0.20	0.0	0.02	0.0	0.07	0.0	0.0
FRVI	1.02	0.42	1.20	1.64	0.53	0.22	0.04	0.04	0.03	0.22	0.22	3.09	0.71	0.0
GABO	0.09	0.02	0.04	0.26	0.06	0.0	0.0	0.01	0.01	0.0	0.01	0.0	0.0	0.0
GATE	0.01	0.0	0.0	0.0	0.01	0.0	0.01	0.0	1.18	9.60	0.01	0.03	0.07	0.06
GALT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0
GATR	0.0	0.03	0.04	0.04	0.01	0.24	0.06	0.11	0.54	1.62	0.0	0.01	0.02	0.06
GEAL	0.0	0.0	0.0	0.02	0.03	0.0	0.0	0.0	0.09	0.64	0.0	0.04	0.22	0.18
HAHY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0	0.0
HELA	0.0	0.01	0.0	0.0	0.20	0.0	2.00	5.80	0.17	2.00	0.82	0.0	0.0	0.0
HIUM	0.0	0.0	0.0	0.0	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
JUBA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.0	0.0
LAOC	2.40	0.13	2.20	2.20	1.21	0.82	1.80	1.32	0.12	0.02	2.80	0.01	0.01	0.0
LAVE	0.0	0.70	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LIBO	0.15	0.81	0.26	0.44	0.01	0.40	0.04	0.01	0.0	0.0	0.0	0.0	0.0	0.0
LYTH	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.10	0.0
MACA	2.50	2.62	1.62	1.20	1.60	2.40	1.00	0.43	0.68	0.0	0.0	0.01	0.01	0.0
MEAR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.22	0.01	0.01	0.06
MEPA	0.41	0.01	0.04	0.0	0.41	0.84	1.02	3.51	3.68	0.02	5.20	0.0	0.0	2.64
MINU	0.0	0.01	0.02	0.01	0.12	0.08	0.04	0.0	0.09	0.0	0.0	0.01	0.01	0.01
OSDE	0.0	0.01	0.04	0.0	0.0	0.0	0.0	0.0	0.01	2.00	0.0	0.0	0.0	0.0
ORSE	0.01	0.0	0.0	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PAPA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.11	0.0
PEPA	1.03	0.30	1.00	0.0	0.02	2.62	0.60	0.43	1.41	0.40	3.40	0.0	0.0	0.0
PESA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0	3.80	0.0	0.01	0.51	1.76
POAM	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.33	0.02
POAN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0	0.0
PONO	0.0	0.10	0.0	0.0	0.0	0.0	0.02	0.01	0.0	0.0	0.0	0.0	0.0	0.0
PYAS	0.31	0.52	0.26	0.06	0.01	0.62	0.06	0.30	0.11	0.0	0.0	0.05	0.01	0.04
PYCH	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.01	0.0
RUAR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.50	0.21	0.29
RUPU	6.20	3.21	6.60	4.00	1.61	5.60	0.22	4.60	1.09	1.00	0.80	0.36	0.40	0.0

Appendix 3 - continued.

SPECIES	ASPEN FOREST					BALSAM POPLAR FOREST						SHRUB FEN		
	Potr-1 N=10	Potr-5 N=10	Potr-2 N=5	Potr-3 N=5	Potr-6 N=10	Poba-1 N=5	Poba-2 N=5	Poba-4 N=10	P-1 N=10	P-3 N=5	P-4 N=5	Will-2 N=14	Will-3 N=9	Will-4 N=9
Forbs:														
SMST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.30	0.53	0.0	0.0	0.0	0.0	0.0
SOAR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.21	0.14	0.0
SOCA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.16	0.01	0.01
STPA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.03	0.0
STEL	0.0	0.0	0.0	0.0	0.01	0.01	0.01	0.01	0.01	0.01	0.0	0.01	0.01	0.01
TAOF	0.01	0.0	0.08	0.06	0.06	0.02	0.01	0.01	0.27	0.06	0.02	0.04	0.02	0.0
TRRE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0	0.0
URGR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.34	3.82	0.0	0.0	0.01	0.0
VIAM	0.02	0.0	0.01	0.01	0.04	0.02	0.08	0.0	0.0	0.0	0.24	0.0	0.01	0.01
VICA	0.24	0.93	0.48	0.02	0.65	0.01	0.0	0.11	0.01	0.0	2.60	0.0	0.0	0.0
Graminoids:														
CACA	0.02	0.01	0.01	0.01	0.34	0.01	0.02	0.05	0.14	0.22	1.84	0.36	0.01	0.0
CAIN	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	1.52	1.66
CXAT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.79	2.21	4.00
CXAU	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.17	0.11	0.0
CXBE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.01	0.0
CXDI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08	0.22	0.0	0.0	0.0	0.0
CXRO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.23	0.01
GLST	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.0	0.0	0.0	0.0
ORAS	0.01	0.01	0.0	0.01	0.10	0.0	0.0	0.0	0.0	0.0	0.0	0.16	0.0	0.0
PHAR	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0	0.0
POAS	0.0	0.0	0.01	0.02	0.02	0.0	0.0	0.0	0.0	0.0	0.0	0.16	0.31	0.01
SCPU	0.01	0.01	0.01	0.01	0.02	0.0	0.0	0.0	0.01	0.0	0.0	0.01	0.0	0.0
Pteridophytes:														
BOLU	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0	0.0
DRYO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0
EQAR	0.0	0.0	0.0	0.0	0.0	0.06	0.23	0.02	0.44	0.62	0.26	0.01	0.03	0.01
EQSC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0	0.0
EQSY	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 4: Size (H=height in cm; BD=basal diameter in mm) and biomass (LB=leaf biomass in g; CAG=current annual growth in g) of the stems of *C. cornuta* selected for the simulated browsing experiment.

0 %				25 %				50 %				75 %				100 %			
H	BD	LB	CAG	H	BD	LB	CAG	H	BD	LB	CAG	H	BD	LB	CAG	H	BD	LB	CAG
123.	6.6	5.13	0.59	154.	9.7	11.31	1.36	164.	11.0	12.25	1.76	131.	10.6	12.77	2.70	155.	13.0	10.42	1.94
216.	14.6	14.03	1.15	117.	9.4	8.32	0.56	98.	7.7	5.06	0.63	112.	8.4	2.73	1.06	120.	9.9	7.11	1.83
220.	15.5	19.70	2.46	130.	9.0	6.16	2.13	153.	12.8	11.80	2.22	136.	11.9	10.84	1.93	155.	13.1	9.66	2.26
204.	10.9	9.43	1.03	133.	10.5	11.03	1.10	137.	10.2	8.48	1.85	149.	11.2	14.45	2.30	115.	11.0	6.28	0.67
181.	11.4	6.79	1.38	120.	7.6	5.56	1.06	135.	9.6	10.00	2.55	114.	9.6	6.02	0.61	65.	7.8	0.56	0.76
198.	13.4	13.53	1.35	152.	10.5	8.90	2.61	140.	11.6	9.09	2.10	80.	6.9	2.76	0.30	149.	11.9	4.60	1.23
240.	13.9	19.16	2.21	167.	12.4	16.91	2.51	105.	7.1	2.78	0.53	101.	8.7	5.28	0.80	160.	14.1	12.34	1.79
87.	6.7	1.12	0.65	188.	12.0	6.26	1.98	124.	9.4	4.99	1.08	88.	6.2	3.70	0.63	94.	7.0	2.37	1.47
108.	7.3	3.58	0.31	145.	10.8	10.30	1.31	132.	10.6	7.68	2.37	153.	12.3	14.48	1.86	99.	8.9	2.15	1.16
216.	13.3	14.74	2.22	84.	7.2	4.10	0.51	141.	11.6	13.64	2.84	173.	9.3	9.18	1.18	156.	9.0	6.93	1.33
77.	7.4	4.41	0.51	200.	13.4	9.97	1.00	164.	10.5	4.98	1.45	152.	9.3	5.91	0.57	161.	9.5	6.71	0.88
119.	9.2	7.73	1.06	160.	9.8	6.75	0.76	127.	10.5	7.62	1.63	160.	9.9	4.82	1.27	130.	10.0	7.74	1.37
95.	6.9	2.06	1.18	198.	12.3	12.12	1.40	190.	11.9	10.93	2.89	214.	12.1	9.64	0.71	144.	11.4	7.49	1.98
112.	7.8	4.99	0.70	149.	10.7	6.64	1.08	131.	8.1	3.26	1.71	244.	13.9	14.63	2.20	150.	11.5	3.83	0.79
166.	14.8	15.84	1.53	187.	12.9	12.25	1.57	155.	8.0	4.26	1.03	178.	10.2	8.74	1.66	261.	16.7	15.49	2.72
132.	12.0	7.04	1.71	131.	10.4	11.09	1.85	116.	7.2	3.15	0.94	129.	10.2	3.28	1.50	99.	6.7	1.94	1.02
160.	7.7	14.95	2.09	178.	10.9	8.30	1.31	135.	9.2	6.03	1.23	185.	11.5	13.80	1.43	154.	9.7	6.82	1.93
119.	8.9	6.62	0.44	132.	9.8	6.90	1.72	228.	14.4	14.20	2.55	164.	9.3	9.55	1.35	176.	11.4	5.75	0.50
128.	11.3	15.32	2.40	144.	11.9	8.38	1.09	183.	11.5	11.30	2.51	167.	10.2	6.57	1.83	239.	14.9	8.49	1.95
143.	7.0	5.51	1.33	162.	13.6	19.06	2.57	138.	9.6	6.71	1.60	118.	8.4	1.93	0.44	160.	12.0	3.77	1.80
113.	8.2	5.34	0.34	140.	11.2	8.61	1.33	209.	13.4	16.79	2.21	172.	10.6	12.86	1.41	230.	13.2	10.24	1.23
245.	15.2	19.25	4.55	186.	12.6	10.26	1.32	180.	10.8	10.35	3.18	235.	15.5	19.93	3.68	147.	10.8	12.71	1.72
113.	8.1	5.65	1.14	156.	10.5	8.91	2.27	212.	13.8	19.13	2.07	185.	13.5	12.89	1.20	130.	9.4	7.00	1.01
132.	14.4	16.55	1.28	160.	10.7	12.19	1.14	211.	14.4	17.40	2.75	198.	13.7	14.53	2.70	171.	9.6	6.41	1.39
66.	8.8	2.94	0.84	157.	10.1	7.08	1.80	207.	12.3	12.99	2.07	214.	10.8	11.76	1.17	130.	9.4	4.16	1.70
179.	10.3	4.68	1.50	193.	12.8	16.24	2.02	194.	11.0	8.43	1.10	153.	9.0	4.82	0.91	200.	13.1	9.09	1.26
100.	10.6	8.04	1.41	185.	11.4	14.00	2.31	233.	13.1	11.62	2.03	168.	9.5	4.72	0.97	150.	11.4	8.87	0.89
71.	6.3	1.07	0.61	180.	13.5	14.43	1.45	214.	13.4	17.55	2.12	164.	10.7	6.29	1.70	150.	9.1	3.96	0.55
162.	10.6	10.53	2.09	126.	7.5	4.90	1.26	152.	11.0	10.59	1.07	140.	8.4	3.37	0.96	137.	8.9	3.04	1.56
113.	8.1	5.65	1.14	169.	10.9	8.35	1.38	158.	7.7	5.85	0.45	216.	14.8	19.03	3.00	210.	12.5	10.33	0.95

Appendix 5: Size (H=height in cm; BD=basal diameter in mm), biomass (LB=leaf biomass in g; CAG=current annual growth in g; TB=total aboveground biomass in g) and age of *C. cornuta* stems in 1m X 1m quadrats (Q) in three aspen forest stands.

QUARTER SECTION OF MWRS Potr-6							SANCTURY Potr-2							SANCTURY Potr-1						
Q	Age	H	BD	LB	CAG	TB	Q	Age	H	BD	LB	CAG	TB	Q	Age	H	BD	LB	CAG	TB
1	10	131.	10.9	4.91	0.89	46.8	4	3	17.	2.8	0.13	0.18	0.4	7	11	69.	5.3	1.97	0.13	7.9
1	11	133.	10.0	2.72	0.68	40.4	4	4	37.	5.2		0.38	1.7	7	3	75.	5.4	1.24	0.44	4.8
1	7	115.	7.2	4.77	0.68	25.8	4	9	34.	3.9		0.10	1.4	7	4	75.	5.6	1.83	0.68	7.6
1	11	120.	11.1	5.03	0.97	57.0	4	7	65.	6.0		0.18	7.9	7	17	119.	9.2	7.73	1.06	31.1
1	11	144.	12.3	6.86	1.32	76.8	4	6	52.	4.7		0.10	3.1	7	3	41.	3.6	1.02	0.08	2.5
1	7	109.	10.2	3.37	1.29	28.0	4	6	42.	6.2		0.26	5.4	7	1	36.	3.4	0.37	0.65	1.0
1	13	82.	7.8	1.57	0.36	18.7	4	4	14.	3.1		0.04	0.5	8	8	110.	10.5	6.18	1.26	35.1
1	14	128.	9.3	5.40	0.98	42.7	4	5	36.	4.2		0.16	2.3	8	10	112.	7.8	4.99	0.70	21.9
1	3	68.	7.0	2.78	2.00	9.1	4	10	121.	9.6	3.43	0.52	37.9	8	10	166.	14.8	15.84	1.53	111.3
1	5	47.	6.2	1.72	0.96	5.8	4	7	75.	6.4		0.48	8.7	8	1	78.	4.6	1.05	2.85	3.9
1	6	43.	6.4	2.59	0.37	8.5	4	1	12.	1.9		0.10	0.1	8	11	123.	6.6	5.13	0.59	20.7
1	1	30.	2.7	0.11	0.26	0.4	4	6	79.	5.3	1.62	0.39	6.5	8	3	60.	5.2	1.12	0.59	3.8
1	3	34.	3.7	0.55	0.23	1.4	4	3	53.	4.3	0.68	0.28	2.2	8	1	74.	4.7	1.06	2.76	3.8
1	4	41.	5.0	0.80	0.26	3.3	4	5	54.	5.7	1.28	0.19	4.9	8	10	41.	4.3	0.40	0.02	2.0
1	3	55.	8.3	0.42	1.03	3.5	4	7	63.	4.9	0.91	0.10	5.8	8	2	20.	3.5	0.23	0.02	0.7
1	2	24.	3.7	0.35	0.23	0.9	4	5	72.	6.2	1.18	0.50	7.4	8	2	19.	2.9	0.24	0.10	0.6
1	11	127.	10.8	1.83	0.43	33.7	4	5	60.	5.1	1.22	0.49	4.9	8	3	17.	2.5	0.06	0.03	0.3
1	11	105.	9.4	4.88	0.86	33.8	4	4	37.	3.5		0.22	1.1	9	7	132.	12.0	7.04	1.71	51.6
1	4	62.	8.5	1.06	1.15	8.1	4	3	51.	3.6		0.33	1.4	9	11	160.	7.7	14.95	2.09	90.2
1	1	14.	2.0	0.06	0.07	0.1	4	4	70.	5.5		0.47	4.2	9	13	119.	8.9	6.62	0.44	37.9
1	4	62.	8.3	1.31	0.82	9.8	4	6	49.	5.6	0.90	0.51	4.9	9	14	148.	8.1	12.45	1.06	85.0
1	3	44.	6.1	0.75	0.42	6.7	4	9	119.	9.5	2.31	0.46	32.4	9	6	143.	7.0	5.51	1.33	48.1
1	6	107.	7.7	2.57	0.66	17.0	4	6	82.	6.0		0.19	10.1	9	5	87.	6.7	1.12	0.65	10.6
1	2	34.	4.2	0.48	0.24	1.6	4	8	97.	7.5		0.17	14.9	9	9	113.	8.2	5.34	0.34	22.4
1	4	53.	5.0	1.19	0.44	4.0	4	7	88.	5.5	1.06	0.44	7.2	9	10	82.	5.5	2.95	0.09	13.4
1	2	64.	5.2	1.27	0.18	4.6	4	10	90.	8.0	0.92	0.29	17.2	9	5	50.	4.1	1.02	0.05	4.2
2	9	123.	10.5	3.84	0.55	42.9	5	12	96.	9.6	3.52	0.78	40.7	9	7	40.	4.1	1.09	0.02	4.3
2	4	112.	8.4	2.99	1.42	16.5	5	9	133.	7.7	3.20	0.49	25.7	9	2	25.	4.1		0.05	0.9
2	10	118.	8.4	4.96	0.54	33.5	5	9	119.	7.8	2.60	0.39	23.8	10	8	245.	15.2	19.25	4.55	133.9
2	5	69.	6.8	1.80	0.93	8.6	5	6	53.	3.0	0.67	0.10	2.3	10	13	218.	16.6	32.80	4.97	202.0
2	11	147.	10.0	3.59	1.07	44.4	5	0	81.	5.1	1.78	0.38	6.8	10	15	132.	14.4	16.55	1.28	104.1
2	11	146.	10.9	6.65	1.69	57.2	5	3	68.	4.8	0.86	0.74	3.4	10	7	32.	5.3	2.87	0.31	8.7
2	8	118.	9.9	2.88	0.45	25.3	5	7	92.	6.3	2.70	0.75	13.7	10	5	66.	8.8	2.94	0.84	14.6
2	4	55.	7.7	1.71	0.66	7.4	5	8	124.	8.1	2.25	0.64	25.2	10	5	179.	10.3	4.68	1.50	37.8
2	4	48.	7.3	1.41	0.54	8.9	5	8	51.	5.3	0.84	0.47	3.0	10	9	108.	7.3	3.58	0.31	21.7
2	8	39.	7.9	1.57	0.46	7.1	5	8	66.	4.3	0.88	0.13	4.2	10	13	77.	7.4	4.41	0.51	23.5
2	3	81.	6.8	2.50	0.66	9.3	5	2	28.	2.7	0.25	0.30	0.7	10	18	85.	7.6	2.35	0.02	17.1

Appendix 5 - continued.

QUARTER SECTION OF MWRS Potr-6							Potr-2							SANCTURY Potr-1						
Q	Age	H	BD	LB	CAG	TB	Q	Age	H	BD	LB	CAG	TB	Q	Age	H	BD	LB	CAG	TB
2	6	95.	6.6	3.29	0.74	13.5	5	3	26.	3.0	0.36	0.12	1.0	10	5	99.	7.2	3.60	1.01	16.1
2	11	148.	9.4	4.37	0.85	42.5	5	3	30.	2.3	0.14	0.03	0.5	10	3	51.	4.6	0.46	0.70	2.6
2	10	141.	10.4	5.82	0.97	57.2	5	5	42.	5.5	0.96	0.40	4.3	10	5	40.	3.8	0.67	0.19	1.8
2	6	130.	9.2	4.11	2.09	21.2	5	8	75.	4.8	0.70	0.05	6.2	10	3	46.	4.5	0.38	0.08	2.5
2	10	105.	6.3	1.86	0.24	13.3	5	8	105.	7.5	1.59	0.36	23.2	10	1	14.	1.8	0.01	0.08	0.1
2	5	93.	6.0	2.23	0.78	8.5	5	8	97.	6.4	2.15	0.49	16.5	10	1	19.	1.7	0.03	0.11	0.1
2	3	50.	3.5	0.58	0.07	2.2	5	8	63.	4.1	1.22	0.15	5.0	10	1	12.	1.5	0.03	0.04	0.1
2	10	112.	8.7	4.88	1.93	30.6	5	9	95.	6.1	2.58	0.44	13.1	11	4	95.	6.9	2.06	1.18	9.8
2	3	34.	3.6	0.36	0.09	1.6	5	8	97.	5.8	0.95	0.31	11.6	11	23	100.	10.6	8.04	1.41	37.1
2	1	42.	3.2	0.82	0.74	1.6	5	1	13.	1.5	0.05	0.12	0.2	11	10	128.	11.3	15.32	2.40	62.7
2	1	8.	1.0	0.03	0.03	0.1	5	1	17.	1.8	0.06	0.16	0.2	11	8	64.	7.4	3.71	0.48	17.5
2	15	111.	7.6	1.33	0.09	15.0	5	1	25.	1.8	0.03	0.18	0.2	11	3	56.	3.7	0.74	0.14	2.5
3	5	68.	6.7	2.68	0.81	8.1	5	1	13.	1.8	0.04	0.07	0.1	11	3	53.	4.3	0.72	0.85	2.5
3	10	100.	10.3	3.19	0.79	30.8	5	1	11.	1.9	0.06	0.10	0.2	11	5	40.	3.8	0.88	0.11	2.7
3	15	105.	10.7	2.65	0.75	39.3	5	6	18.	2.4	0.18	0.15	0.6	11	4	82.	5.2	1.75	0.53	7.5
3	4	76.	5.5	0.47	0.11	4.5	5	2	49.	3.3	0.28	0.79	1.5	11	1	41.	3.0	0.38	0.09	1.1
3	2	65.	4.2	1.28	1.25	3.3	5	4	64.	4.5	0.94	0.36	3.3	12	10	162.	10.6	10.53	2.09	64.7
3	6	70.	7.3	2.33	0.64	10.3	5	2	39.	3.6	0.55	0.54	1.7	12	8	113.	8.1	5.65	1.14	25.5
3	5	43.	8.2	2.12	0.67	11.6	5	3	59.	4.3	0.93	0.52	3.7	12	2	54.	6.2	0.48	0.17	2.8
3	8	44.	5.6	1.47	0.26	4.8	5	4	59.	4.5	0.92	0.20	3.8	12	3	71.	6.3	1.07	0.61	6.0
3	1	11.	1.4	0.03	0.05	0.1	5	3	52.	4.1	0.50	0.61	2.2	12	5	70.	6.0	2.60	0.30	9.8
3	9	71.	11.4	2.61	0.57	8.8	5	4	22.	2.5	0.06	0.07	0.4	13	2	7.	1.2	0.04	0.01	0.1
3	11	59.	6.4	2.30	0.50	7.3	6	7	71.	7.4	3.79	0.81	13.7	13	2	76.	6.0	1.27	1.81	6.6
3	13	121.	9.3	2.87	0.65	30.1	6	12	42.	5.3	1.08	0.14	3.7	13	8	105.	8.6	6.75	1.77	27.1
3	5	53.	5.2	1.24	0.29	4.3	6	10	67.	5.4	1.16	0.15	5.0	13	13		10.0	10.20	30.62	85.7
3	3	50.	4.7	1.90	0.43	4.4	6	12	118.	9.9	6.11	1.18	56.6	13	9		11.0	11.86	2.44	62.8
3	3	33.	3.6	0.53	0.06	1.7	6	10	120.	9.9	5.68	0.95	39.5							
3	1	32.	3.4	0.41	0.52	0.9	6	9	85.	5.7	2.11	0.42	9.4							
3	2	24.	3.0	0.30	0.18	0.8	6	2	23.	2.7	0.23	0.15	0.5							
3	4	27.	5.5	0.43	0.02	4.5	6	2	27.	2.5	0.23	0.19	0.8							
3	11	93.	9.2	4.52	0.84	26.2	6	2	22.	2.0	0.22	0.10	0.5							
3	11	141.	12.1	5.80	0.98	57.2	6	1	6.	1.4	0.05	0.03	0.1							
3	4	38.	6.0	1.22	0.25	4.5														
3	3	12.	3.6	0.49	0.03	2.1														
3	1	19.	2.4	0.15	0.21	0.4														
3	5	53.	7.5	2.74	0.96	10.5														
3	8	24.	4.2	0.83	0.07	2.6														
3	10	49.	6.5	0.75	0.16	5.4														
3	7	89.	8.6	3.89	0.79	18.3														
3	1	19.	2.2	0.15	0.22	0.4														

Appendix 6: Size (H=height in cm; BD=basal diameter in mm), biomass (LB=leaf biomass in g; CAG=current annual growth in g; TB=total aboveground biomass in g) and age of *A. alnifolia* stems in two aspen forest stands.

SANCTUARY (Potr-1)						QUARTER (Potr-6)					
Age	H	BD	LB	CAG	TB	Age	H	BD	LB	CAG	TB
1	39.	3.4	0.22	0.75	1.2	36	124.	13.2	0.67	0.37	64.3
14	120.	11.7	1.58	0.75	38.5	9	122.	12.2	0.91		65.8
9	140.	10.2	2.07	0.85	38.1	20	110.	10.8	0.78	0.21	39.1
11	142.	15.1	3.11	2.19	102.3	9	84.	9.0	1.93	1.02	20.9
13	115.	9.2	0.47	0.18	30.9	24	136.	22.1	4.52	1.94	184.3
13	105.	10.1	0.88	0.13	33.6	32	193.	19.5	5.58	1.67	270.2
18	128.	11.5	1.73	0.44	58.8	24	166.	16.5	3.13	2.07	162.9
8	145.	9.9	1.63	1.17	45.9	9	74.	8.4	0.70	0.23	17.0
17	144.	13.1	2.54	1.97	87.0	8	67.	8.4	2.04	0.71	16.1
1	22.	2.1	0.12	0.21	0.3	22	13.	5.5	0.09	0.03	0.9
2	16.	1.8	0.13	0.07	0.2	7	23.	4.3	0.16	0.03	1.2
7	116.	10.9	1.83	0.78	42.8	2	26.	3.2	0.44	0.27	0.9
12	212.	16.5	3.12	0.73	131.6	2	19.	2.2	0.03		0.2
5	95.	5.3	1.54	0.15	11.9	2	19.	1.7	0.12	0.03	0.3
8	78.	5.2	1.15	0.62	7.6	1	13.	1.9	0.11	0.08	0.2
12	74.	6.9	1.45	0.58	16.6	1	7.	1.4	0.04	0.04	0.1
13	112.	7.0	3.07	2.30	25.6	1	8.	1.5	0.07	0.05	0.1
14	115.	8.4	5.10	2.02	35.9						
9	121.	8.9	2.44	0.58	39.2						
11	167.	8.8	1.81	0.46	52.6						
12	125.	8.6	4.30	1.53	36.9						
11	133.	8.0	3.81	1.98	30.6						
8	94.	5.7	0.97	0.50	10.1						
23	292.	8.7	4.55	1.49	150.8						
9	129.	6.4	2.33	1.13	20.6						
7	130.	6.5	1.82	0.96	17.0						
6	58.	3.6	0.77	0.14	3.9						
3	50.	2.8	1.12	0.98	2.8						
2	53.	2.7	0.58	0.19	1.6						
2	45.	3.0	0.40	0.53	1.5						
1	42.	2.4	0.20	0.01	0.8						
3	46.	2.0	0.61	0.10	1.3						
2	56.	3.3	0.82	0.49	2.7						
3	31.	2.2	0.62	0.10	1.4						

Appendix 6 - continued.

SANCTUARY (Potr-1)						QUARTER (Potr-6)					
Age	H	BD	LB	CAG	TB	Age	H	BD	LB	CAG	TB
2	28.	1.7	0.37	0.01	0.7						
4	35.	2.6	0.25	0.21	0.9						
3	37.	2.6	0.28	0.16	0.9						
1	10.	1.1	0.03	0.03	0.1						
44		45.0									
26		15.0									
46		45.0									
34		27.0									
34		32.0									
36		19.0									
29		18.0									
33		15.0									
32		13.0									
11		12.0									

Appendix 7: Size (H=height in cm; BD=basal diameter in mm), biomass (LB=leaf biomass in g; CAG=current annual growth in g; TB=total aboveground biomass in g) of *S. planifolia* and *C. stolonifera* stems in the quarter section of the MWRS.

S. planifolia (Will-2) tall clump					*S. planifolia* (Will-2) small clump					*C. stolonifera* (P-1)				
Age	H	BD	LB	CAG	TB	Age	H	BD	LB	CAG	TB	H	BD	LB	CAG	TB
3	106.	8.7	3.06	6.29	21.5	5	51.	11.1	1.15	0.55	14.6		5.5	1.77	1.60	3.4
6	126.	11.6	1.58	0.20	44.8	4	36.	6.6	0.15	0.01	3.2	50.	4.5	2.13	0.17	2.3
5	106.	9.5	2.73	1.27	24.8	8	55.	10.5	1.50	0.36	20.4	48.	5.2	1.95	0.28	2.2
7	116.	10.7	4.55	2.77	33.3	6	55.	9.4	0.81	0.31	12.5	67.	4.8	1.37	0.68	2.0
8	175.	13.5	7.04	4.76	91.2	7	48.	7.5	0.97	0.40	8.8	89.	9.6	3.05	0.32	3.4
4	175.	12.2	6.61	5.15	69.1	8	58.	10.8	2.39	0.92	18.8	78.	7.9	5.34	0.86	6.2
8	165.	13.6	5.52	3.65	94.1	5	58.	8.8	2.97	0.96	17.7	47.	4.9	1.72	0.18	1.9
8	182.	15.1	13.62	5.15	151.1	7	66.	10.8	2.50	0.71	25.7	62.	4.4	1.80	0.20	2.0
7	152.	12.8	7.58	3.83	67.4	4	60.	6.7	1.04	0.27	6.1	75.	6.0	2.10	0.35	2.4
7	149.	15.0	6.58	2.55	77.0	2	41.	6.1	0.82	0.23	4.1	66.	8.8	1.39	0.08	1.5
4	156.	12.6	5.70	3.08	61.5	7	48.	5.5	0.59	0.07	4.6	86.	5.8	3.81	0.62	4.4
8	175.	12.0	5.50	3.78	71.8	8	72.	10.4	3.98	1.84	27.0	45.	4.0	1.19	0.14	1.3
6	152.	11.9	4.40	1.95	57.4	3	28.	4.5	0.12	0.02	1.9	50.	4.0	0.69	0.19	0.9
8	92.	9.0	2.08	0.70	24.5	6	53.	7.5	0.90	0.23	9.5	70.	7.4	1.56	0.37	1.9
8	168.	8.9	13.10	4.52	120.5	8	70.	15.9	5.17	0.77	60.7	59.	4.5	1.44	0.05	1.5
7	95.	12.8	2.65	1.76	25.0	8			1.35	0.22	15.3	106.	10.0	2.71	0.72	3.4
7		10.3	3.67	1.09	28.2	8	53.	9.6	1.18	0.37	13.4	20.	2.5	0.17	0.30	0.5
7	140.	7.5	3.64	2.49	23.9	8	58.	10.9	2.58	0.82	23.1	39.	4.0	0.51	0.22	0.7
8	162.	15.0	8.66	4.49	111.9	5		8.1	0.29	0.22	7.7	18.	2.7	0.14	0.01	0.1
7	160.	13.7	9.44	8.52	63.1	8	48.	9.9	0.60	0.26	8.8	33.	3.2	0.52	0.37	0.9
6	179.	12.8	10.36	4.27	92.8	7		10.0	0.79	0.12	10.0	39.	3.9	0.68	0.07	0.8
7	167.	11.1	7.08	4.07	73.6	4	610.	9.0	2.09	1.67	16.1	45.	3.5	0.69	0.51	1.2
7	147.	11.6	4.47	2.24	42.2	7	52.	9.1	1.46	0.51	13.9	42.	3.5	0.92	0.09	1.0
16	252.	39.0	37.32	23.40	794.8	8	57.	10.7	1.66	0.82	18.4	32.	2.2	0.22		0.2
16	175.	32.0	24.56	13.29	460.4	5	49.	7.7	0.14	0.15	5.9			6.76	0.31	7.1
												42.	4.3	0.07		0.1
												29.	3.6	0.09	0.02	0.1
												26.	2.9	0.45	0.08	0.5

Appendix 8: Selected photographs illustrating field work.

Photo 1: Understory vegetation in the aspen forest stand Potr-1 in the sanctuary. *C. cornuta* with heights up to 2.5 m was the dominant shrub species.

Photo 2: Understory vegetation in the balsam poplar forest stand P-4 in the sanctuary. The field layer is composed of numerous tall herbs, with *A. nudicaulis* being the most abundant. Note in the background the transition to aspen forest with a higher tall shrub component.

Photo 5: A steady companion - elk cow Bell browsing in the aspen forest stand Potr-6 in the quarter section.

Photo 6: System of roots and underground stems of a *C. cornuta* clone. An old root crown can be seen in the foreground. The origin of the clone could not be traced back further because older woody structures had disintegrated.

Photo 4: Example of a heavily browsed *A. alnifolia* stem from the quarter section. Leaf clusters grew along the old central stem. All twigs were consumed and no new ones were produced during the 1983 growing season.

Photo 3: Heavily browsed *C. cornuta* stem from the quarter section. The hedging was produced by the dying back of browsed twigs. New leaders then emerged from (adventitious) buds. Spreading branches were prevented from developing.